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AN INTRODUCTION TO THE STUDY OF THE COMPARATIVE ANATOMY OF ANIMALS

BY

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VOL. I.

ANIMAL ORGANISATION. THE PROTOZOA AND CŒLENTERATA

SECOND EDITION, REVISED

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PREFACE

In the following Introduction to the study of the Comparative Anatomy of Animals, I have necessarily been guided by the requirements of the elementary examinations at the leading universities of Great Britain.

Having found by experience that beginners find great difficulty in apprehending the full meaning of the cell-theory at the commencement of their studies, I have departed from the course usually pursued in lectures and practical instruction, and instead of beginning with the study of cells, I have taken the common frog as a type of animal organisation. The general anatomy of the frog is first described in some detail; the microscopic structure of its organs and tissues is next explained, and then the cell-theory and the phenomena of the cell-division are dealt with. In this way I have attempted to lead the student gradually from familiar to new and unfamiliar conceptions.

I have attempted, as far as possible, to verify by personal observation the statements of fact contained in this book, but want of time and opportunity has prevented me from repeating the long and laborious researches of many investigators on such subjects as the reproduction of the Protozoa. Where personal observation has been wanting I have tried to give an adequate account of the best and most recent researches on the subject. In certain cases, however, I have preferred the results of older to those of more recent observers. For example, I have adhered to Maupas' account of the phenomena of conjugation in the Ciliata, because in my judgment the results of the latest researches on this matter require independent confirmation before they can be held to overthrow the results of such careful and consistent work as that of Maupas. Since this book is in part a record of my own observations and not wholly a compilation, I have in several cases departed from the accepted accounts of certain phenomena. Thus the description of the truncus arteriosus

of the frog is based upon models made from my series of sections, and the account of the histology of Hydra is largely new, and based upon my as yet unpublished researches. I have not thought it desirable to burden the elementary student with a list of references to literature, and I must ask original authors to pardon me for making use of their facts and arguments without acknowledgment. But in every case in which figures have been taken from published works full acknowledgment is made. The illustrations have been drawn specially for this book; many by Mr P. J. Bayzand, the skilful artist of the Linacre Department at Oxford. Others are by my friend and pupil Mr E. H. Schuster of New College, Oxford, and the rest have been drawn by myself. Where not otherwise stated the figures are from my own sketches and preparations.

There is a considerable difference of opinion as to the limits of *elementary* teaching in Comparative Anatomy. For my own part, I consider that the more elementary the teaching is in this subject the fuller it should be, and I have not hesitated to enter fully into details where a detailed description seemed necessary, and have discussed certain questions of theoretical importance at considerable length. Students seldom begin the study of Comparative Anatomy at an early age, and they should never begin it until they have mastered the elements of Physics and Chemistry. I have therefore addressed myself, not to children, but to persons whose education is well advanced, and whilst I have tried to write simply and intelligibly, I have not attempted to evade the difficulties of technical language. All technical terms, where used for the first time, are printed in thick type, and are sufficiently explained in the context.

Whilst the faults of this book are entirely my own, I must attribute any merit it may possess to the influence of the three successive occupants of the Linacre chair of Comparative Anatomy at Oxford under whom I have had the honour to serve, the late Professor H. N. Moseley, Professor E. Ray Lankester, and Professor W. F. R. Weldon. Nor must I forget the many lessons I have learned from my whilom colleagues at Oxford, Professor W. Blaxland Benham and Professor E. A. Minchin.

The present volume deals with animal organisation as represented by the Frog, with the Protozoa, and the Cœlenterata. The second volume will deal with the Cœlomate Metazoa. I had hoped to bring out the two volumes simultaneously, but have been called out on military duty since the outbreak of the war in S. Africa, so the completion of the second volume has been delayed.

GILBERT C. BOURNE.

THE BARRACKS, TIPPERARY,
March 1900.

PREFACE TO THE SECOND EDITION

IN the course of the nine years that have elapsed since this volume was published many and noteworthy additions have been made to all branches of Zoological Science. Consequently a new edition, embodying such important discoveries as may properly find a place in an elementary text-book, has become necessary. The original plan of the work has not been altered, and many of the chapters remain in practically the same state as in the first edition. The portion of Chapter III. relating to Mitosis, the Maturation of the Ovum, Spermatogenesis and Fertilisation has been rewritten, as has also the chapter on Monocystis. A considerable amount of new matter has been introduced into the chapters on Amœba and Paramecium, and the life-history of *Copromonas subtilis* has been substituted for Dallinger and Drysdale's doubtful account of the life-history of Bodo. In order that the volume may be more serviceable to medical students, who form the majority of the students of Elementary Comparative Anatomy in this country, I have added a chapter on Malaria and the life-history of the Malarial Parasite which will, I hope, afford a useful introduction to the study of the Pathogenic Protozoa. As the volume seemed to be rather overweighted with descriptions of Protozoa, it was my intention to omit the chapters on Actinosphærium and Badhamia, but on the advice of friends

they have been retained, and in view of the great importance of the study of unicellular organisms at the present time, an apology is scarcely needed for devoting a somewhat disproportionate amount of space to them. My thanks are due and are hereby tendered to Professor G. H. F. Nuttall and Mr A. E. Shipley, Fellow of Christ's College, Cambridge, for permission to copy their excellent figures of the female, larva, and mouth parts of *Anopheles maculipennis*. To Dr J. W. Jenkinson of Exeter College, Oxford, for advice and assistance in the chapter relating to Cytology, and to Mr C. Clifford Dobell, Fellow of Trinity College, Cambridge, for much advice and for permission to reproduce his figures illustrating the structure and life-history of *Copromonas subtilis*.

GILBERT C. BOURNE.

SAVILE HOUSE, OXFORD,
May 1909.

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COMPARATIVE ANATOMY

INTRODUCTION

It is necessary, even in the study of Natural Science, to have something of the nature of a creed, an abiding belief in some fixed principle, which may regulate and give coherence to the mass of information and ideas which we accumulate in the course of our studies. Without such a belief to guide us we embark on our journey of investigation without rudder, compass, or pilot.

In those sciences which occupy themselves with the explanation of the existing order of things on the earth, the fundamental beliefs are, firstly, that the course of Nature has been uniform—that is to say, that in past times the same forces have operated, possibly with varying intensities, but always in the same manner as those which are in operation to-day. Secondly, that that which is, is the outcome of that which has been, and is the forerunner of that which will be. The history of the world and its inhabitants presents itself to our imaginations as an unbroken series of successive states, each differing somewhat from its predecessor and successor, but as truly derived from its predecessor as the child is derived from its parent, and as truly the antecedent of its successor as the parent is the antecedent of the child. This belief is what we express by the word *Evolution*.

The Science of Comparative Anatomy is founded on these principles. It believes that living things, ever since their first appearance on the earth, have been essentially the same as they are now, and that the concourse of living animals which now peoples the globe is the result of a long-continued process of evolution, reaching far back into geological time. The assemblage of animals at any given period of the earth's history, with all its diversities of form, habit, and structure, was directly descended from the somewhat different assemblage of the preceding period, and, in its turn, gives rise to the assemblage of the period next following, just as one generation of men

succeeds another, every generation differing somewhat, both collectively and in the individual characteristics of its component members. In fact, the successive generations of mankind are but a part of the successive generations of living beings; and, whilst we use them as an illustration, we are only specifying a part of that universal evolution which it is our business to trace more closely.

Whilst these principles of uniformity and evolution must be our guides through the very intricate paths of the study of animal organisation, it must not be supposed that they are obvious and elementary truths, which can be arrived at by *a priori* reasoning. On the contrary, they have been attained to only as the result of an immense amount of study and reflection on the details of animal organisation, and they cannot be apprehended without a very considerable amount of study and reflection on the part of every individual. It is the object of the present course to justify our belief in these principles by the study of just so much of the structure and development of certain animals as will suffice to bring conviction to our minds.

Superficially, the animal world seems to be in a condition of comparative stability. The least observant person already recognises in early childhood a considerable number of kinds of animals. The individuals of each kind are approximately like to one another, they come and go, are born and die, but they leave behind them progeny which continues to exhibit the same characteristics of form and structure, and we learn from books that these same kinds of animals with which we are familiar, have existed with these same characteristics ever since man began to describe the natural objects by which he is surrounded.

Daily experience and written record, therefore, combine to impress upon our minds the notion of the fixity of the form and structure of the different kinds of animals. The fixity is not absolute, for we recognise individual differences between animals of the same kind, yet these differences are so small and the likenesses so great that we have no hesitation in describing animals having such and such characters as being of one kind, or, as zoologists say, of one **species**.

We observe, then, that the earth is tenanted by countless species of animals, that each species remains constant and has remained constant as far back as human records go, yet we

are asked to believe that this constancy, so evident to our experience, is a delusion, and that change is the rule in the animal world. If we come to think of it, change is the rule, even among individuals. The individual man passes from infancy to childhood, from childhood to youth and manhood, and finally to senility and death. All these stages in his career mean change, and we recognise the same changes as occurring in animals. Further reflection assures us that even during the stages when the body seems to have arrived at a condition of stability of some duration, there is daily change going on. A man gains or loses in weight according to the amount of work he does and the amount and form of nourishment that he takes. It is a familiar fact that if we would do an increased amount of work we must take a larger amount of food, that if we do less work we must take less food, or pay the penalty of becoming stout. The same thing applies to the animals which we domesticate and compel to work for us, and though we cannot follow the steps so closely in the case of wild animals, we have no doubt that they too are subject to the same conditions.

In short, animal life is the outcome of a never-ceasing series of chemical changes. An animal is constantly taking in substances as food, converting these substances into the living material of its own body, and then, when it exhibits energy of any kind, this living material undergoes chemical change, is broken down into substances of comparatively simple chemical constitution, which, being of no further use in the body, are forthwith expelled as excreta.

This condition of constant exchange of material is characteristic of all living things, whether animal or vegetable, and marks them off sharply from dead or inanimate objects. A living organism is constantly manifesting energy, whether in the form of motion or of heat. The source of this energy is chemical change in the constituents of its body. These constituents, of complex and unstable chemical constitution, enter into combination with the oxygen of the air, are broken down into substances of less complex and more stable constitution, which are ejected from the body, and if the loss thus occasioned were not made good the body would waste away. The loss is made good by food, which is converted into new living tissue to be broken down afresh; and so the process goes on.

During infancy and youth the gain by food is greater than the loss, and so the animal grows; during maturity the income and expenditure are practically balanced. In old age the expenditure is in excess of the income, so that decay sets in and the organism finally perishes.

It perishes, but not entirely, for it has the capacity, which is another great characteristic of living things, of reproducing its like. On reaching maturity a part of it, generally an infinitesimal part, is separated: this part lives, absorbs nourishment and grows into a new organism which resembles in every essential particular the parent form from which it was separated. It is in virtue of the resemblance of the offspring to the parent, commonly called **heredity**, that species retain that fixity of form and structure to which we have alluded.

These facts are sufficiently familiar to all, but the consequences of them are very seldom understood. The fact that food is necessary, both to animals and plants, makes them dependent on those external physical conditions which are generally summed up in the term **environment**. Plants are as much, and even more dependent on their environment than animals, but their relations to it are quite different.

A plant is able to obtain its food in a manner which is quite impossible to animals.* The substance of which all living things, both plants and animals, are composed is known as **protoplasm**. We shall study it more closely hereafter, and need only state here that it is an albuminous body of great chemical complexity, composed of the elements Carbon, Hydrogen, Oxygen, Nitrogen, Sulphur, Phosphorus. It is obvious that an organism, in order to repair the material of its body must be supplied with all these elements. Plants are able, in virtue of the property possessed by their green colouring matter, **chlorophyll**, to obtain their carbon from the minute quantities of carbon dioxide present in atmospheric air. So part of their food is gaseous. The other constituents they obtain in solution in water, by means of their roots, so that the remainder of their food is absorbed in a liquid form. If a plant is supplied with a weak solution of certain mineral substances, and is kept in the air and in sunlight (for chlorophyll is only active in sunlight), it is able to construct protoplasm out of these simple mineral and gaseous com-

* With the few exceptions to be mentioned later.

pounds. But no animal can do this. An animal supplied with the substances suitable for plant food would starve and perish from inanition as quickly as if they were withheld from it. It must have food already elaborated, in the first instance through the agency of plants. It requires, in addition to water, proteid or albuminous substance whether derived from vegetable or animal sources, starches and sugars, and fats. These are solid substances which the animal takes into itself, or, as we say, **ingests**, and elaborates within its body into the more complex substance of living tissue.

It is by reason of this fundamental difference in nutrition that plants and animals differ so widely from one another in structure. The plant, dependent on gases and liquids for its food, seeks to expose as much surface as possible to these media. It spread its leaves in the air, and thus presents a great surface for the assimilation of carbon from the carbon dioxide of the air. Its roots penetrating into the earth seek out the water which, percolating through the soil, has dissolved and holds in solution the mineral matters necessary to its sustenance. Fixed thus in the earth the plant is independent of locomotion, of sense organs, of means of capturing and swallowing its food, and, though it is true that some of the lowest plants are locomotory, the proposition just stated holds good for the vast majority of the members of the vegetable kingdom.

Animals, on the other hand, are under the necessity of moving in search of their food. They require the means of recognising it, of seizing and swallowing it, and since they do take it into themselves or swallow it, they require some sort of cavity or receptacle in which it may be contained and further elaborated. Clearly, then, the relations of an animal to its environment are far more complex than those of a plant ; and they are the more complicated because animals stand in every kind of relation to one another, and are endowed, as the case may be, with special powers of offence or defence, with means of protection, concealment, attraction, and even of deception.

Looking at an animal from a general point of view, and studying its necessities to some extent in the light of our own, we may enumerate the several activities indispensable to its existence.

Each of these activities is effected, in higher animals like

ourselves, through the means of a special living mechanism, and each such mechanism is called, in technical language, an **organ.** An organ is not, as a rule, a simple homogeneous substance of like material throughout, but is a composite structure, formed of special kinds of living material, and each kind of living material entering into the composition of an organ is called a **tissue.**

Since an animal is locomotory, or at least endowed with the power of movement, we may expect to find a special set of motile organs or tissues, and we find them in **muscular tissue.** The substance commonly known as flesh is muscular tissue. It exhibits in an eminent degree the phenomenon of **contractility**—by which is meant the power of decreasing in one dimension whilst it increases in another. There must be no confusion between the vital muscular contraction and the physical phenomenon known by the same name. Put the poker in the fire, and it will expand as it becomes heated; remove it and it will contract as it cools. In expansion and in contraction its bulk increases or diminishes in every dimension, and that to so slight a degree that special means are required to measure the change. But nobody ever heard of a poker suddenly, as the result of a shock or blow maybe, diminishing in length to a very appreciable amount, and at the same time swelling up in the middle, so that its bulk remained the same, but its shape altered. This, however, is what a muscle does, and everybody can observe this property in the biceps muscle of his own arm.

Muscles contract with considerable force, and, by pulling or pushing on or against some fixed object, effect movements of the animal's body. In many animals they are attached to a system of levers, which form a part of what is known as the skeleton of the animal. In ourselves, and in animals allied to us, these levers are internal, and clothed by muscle; but in many other animals such as crabs and lobsters, spiders and insects, the hard movable parts are outside and the muscles inside. The skeleton, when present, is a very important part of the animal economy, and besides affording a *point d'appui* for the muscles, it gives support to the whole body and protects some of the delicate organs from injury. Skeleton and muscles taken together form far the greater part of the bulk of the higher animals.

An animal ingests bulky food in a crude state ; before this food can be made serviceable, and can be converted into actual living matter, or stored up in some form in which it may be serviceable hereafter (*e.g.* in the form of fat), it has to undergo a process of chemical elaboration. The great majority of animals have a special aperture for taking in food, **the mouth**. This is very commonly furnished with special mechanisms for seizing and comminuting the food—viz. with **jaws** and **teeth**. The mouth leads into a more or less capacious tube, **the gut**, in which the process of elaboration goes on. The gut is a sort of laboratory, and is provided with the necessary stock of chemical solvents poured into it from special receptacles, **the glands**, with which it is abundantly provided. The substances poured in by the glands are known as **secretions** : they act chemically upon the food, rendering it soluble and capable of passing through the relatively thin walls of which the gut is composed. Those parts of the food which are insoluble are expelled, usually through a special aperture, the vent or **anus**. The food, altered and rendered soluble, passes through the walls of the gut. It has to be distributed to all parts of the body—many being situate at some distance from the gut. To this end we find a mechanism for distributing the nutriment to all parts, commonly in the form of a system of tubes, containing a fluid in which certain solids are suspended. There are two such fluids in ourselves, the blood and the lymph ; each with its proper system of channels and vessels. By the blood and the lymph the nutriment is conveyed to every tissue, and in the tissues themselves it undergoes those further changes which may be described as transformation into living substance of unstable composition and high potential energy. The blood is kept in movement by the contractions of a hollow muscular sac, the heart. The blood, however, is much more than a carrier of nutriment. The complex living substance liberates energy in undergoing further chemical change, on breaking down again into simpler substances, and this change is at the bottom a process of oxidation. A supply of oxygen is therefore necessary in every part of the body, and this is provided for by a special **respiratory** mechanism. There are various kinds of respiratory mechanisms, but they are all alike in this respect, that they afford a means of interchange between the gases dissolved in

the blood and those contained in the air (or, in the case of aquatic animals, air dissolved in water). In ourselves the respiratory mechanism consists of a pair of sacs, the lungs, with thin walls in which exceedingly fine blood-vessels ramify. By means of special muscular arrangements the lungs are alternately expanded and compressed like bellows; air rushes in and out, and in the cavities of the lungs it is separated by such very fine membranes from the blood that exchange of gases readily takes place. The blood absorbs oxygen from the air and carries it to the tissues; the oxygen combines with tissue materials; these, being oxidised, break down into simpler substances and liberate energy. The simpler substances must be got rid of, or they would accumulate and clog the machine. The blood again is the agent for carrying away waste matter. The principle waste matters are carbonic acid, water, and nitrogenous bodies—*e.g.* urea. Carbonic acid, a gas, is got rid of by the lungs; water by the lungs, the skin and the kidneys; the nitrogenous bodies by the kidneys. Thus we find that there are special mechanisms for getting rid of waste matters, or **excreta**, as they are called, and we recognise the skin and kidneys as excretory; the lungs are in part excretory, but they also serve for introducing oxygen into the system.

Thus there is a continual exchange of material going on in the animal body. Fresh material is coming in, waste material is going out, and the blood is the medium of exchange. It carries the fuel to the places where it is wanted, and removes the ashes; it also carries the torch, in the shape of oxygen, which kindles the flame and burns up the material. The whole series of exchanges is expressed by the word **metabolism**. We can distinguish two phases of metabolism, the building-up processes from food to living matter, called **anabolism**; the breaking-down processes, with formation of carbonic acid, water, and urea, called **katabolism**. The several organs which we have spoken of are not always in action, nor do they act at haphazard. On the contrary, they perform their functions when and as they are required, and that in a definite order and sequence. They work harmoniously, not each organ for its own ends, but all combining for the good of the whole individual of which they form the parts. This co-ordination of functions is effected by the **nervous system**, which may be likened to a great telegraph system with a central office from

which wires pass to every part. The wires are the **nerves**, the head office is the **central nervous system**; in ourselves **the brain** and **spinal marrow**. There are wires for bringing messages in (**afferent nerves**) and wires for taking messages out (**efferent nerves**), and messages are continually travelling along them. News comes to the central office of some change or occurrence without or in some part of the body, and forthwith messages are flashed out to the appropriate parts, ordering muscles to contract, glands to secrete, etc. But how are the messages sent? All living substance is to a certain extent *irritable*—that is to say, it responds to a shock or stimulus of any kind, and this response is not the passive result of pull or push, but an active manifestation of energy, often disproportionate to the amount of the disturbing influence. Nervous tissue is the irritable tissue *par excellence*, and stimuli are conveyed to it by means of the organs of special sense — viz. touch, sight, hearing, smell, and taste. Touch organs are distributed all over the skin, in the form of minute bulbs, each connected with a fine nerve fibril. The eye is the organ of sight, and it consists essentially of end organs of extreme minuteness, which are capable of being affected by luminiferous undulations of ether. The bulk of the eye in ourselves is made up of arrangements for focussing the light on the actual end organs. The ear similarly has end organs, which are affected only by sound waves, and in addition, there is an apparatus for communicating the vibrations of the air to the end organs. Smell and taste are localised patches of end organs of similar kind. Beyond these we may speak of a muscular sense, and a temperature sense.

Through these channels comes all the information that we have of the outside world, and, in addition, a great deal of information comes to our brains about the working operations of our own bodies, but this information is not recorded in our consciousness and we are not aware of its being sent. The brain, however, does the needful, and sends out the messages appropriate to keeping up the working of the machine.

The various organs must not only work together, but must also be held together, and they are bound up and connected by a special form of tissue appropriately called **connective tissue**. Moreover, every free surface of the body and its organs is covered by a protecting membrane known as an

epithelium, or if it is an internal surface an **endothelium**, of which more hereafter. Finally, there is the **reproductive system**. The animal casts off a minute and formless part of its substance, and this part under appropriate conditions grows, assumes the shape and structure of the whole form which it was cast off, and becomes a new animal, like to its parent. Reproduction is a complex process which will be better understood at a later stage.

An animal, then, of a degree of organisation comparable to our own, has muscular, skeletal, digestive, glandular, blood-vascular, respiratory, excretory, nervous, sensory, and reproductive organs, each performing its special function, and all working together to the ends of the individual. The detailed study of the functions of the animal body, and the exposition of the mechanisms and chemical actions by which those functions are performed belongs to the science of animal physiology. We are only concerned with the materials of which the organs are constructed, what are their form and composition, how they are combined, and how the organs are fashioned and put together in different kinds of animals. In short, the comparative anatomist is concerned with the architecture of the building, and gives but a passing heed to the uses to which the parts of the building are put.

Comparative anatomy, then, is the science which treats of the architecture of animals, and we shall see that just as there are several styles of architecture, Classical, Byzantine, Gothic, etc., each with its subdivisions, as Gothic into Pointed, Perpendicular, Decorated, etc., so there are several styles of animal architecture, and in each style there is infinite variety, though the general plan, the "motive," is the same.

But even as all buildings resemble one another in the most general way because, whatever their style, they are put to similar uses, so do all animals resemble one another in a very general way because, being animals, they have similar functions to perform, and those functions are performed by analogous organs.

Not by any means, however, by organs which have any degree of exact similitude. Let us compare two or three familiar kinds of animals with one another; a dog, a fish, and a lobster. The fish (say, a cod or pike) and the lobster are both aquatic animals, and it might be supposed that they

would more nearly resemble one another than do the fish and the dog. But the slightest analysis of their structure will show that they do not.

The fish has a distinct head provided with jaws, and in the jaws are teeth. On its snout are the openings of the organs of smell, usually called olfactory organs, and they have the form of a pair of pits with external apertures. Behind them is a pair of eyes, placed in sockets, movable by muscles fixed on a definite hollow eyeball. Behind the eyes we find, embedded in the skull, a pair of organs of hearing—the auditory organs. All these structures are present in the dog also, and though the details differ largely, the general arrangement is the same. The muscles which move the eyeballs are almost identical. In both the dog and the fish the head is largely formed of a bony and gristly case or box, which contains a mass of nervous structure—the brain. The fish has no distinct neck, the head passing without any distinct intervening region into the trunk or body. The dog has a neck. Both the fish and the dog have a distinct backbone, or, as anatomists call it, a **vertebral column**, composed of numerous short bony joints or pieces, arranged in a row down the middle of the back, ending behind in a tail and jointed in front to the brain-case or skull. And we find that in both dog and fish there is a little arch placed on the top of each joint of the backbone, and in the canal formed by all these arches there lies a long nervous cord, the spinal marrow or spinal cord, which is directly continuous in front with the brain. The dog has two pairs of limbs used for walking and running, the fish has two pairs of fins used as aids in swimming. The fins are not at all like the dog's legs, but they occupy the same relative positions, and are comparable to some extent. Other noticeable features show considerable differences between dog and fish. The dog has a coat of hair covering its body—the fish a coat of scales. The dog breathes air by lungs, the fish breathes water by gills, which are really a series of apertures passing from the throat to the exterior, the walls which separate the apertures being covered with folds of tissue richly supplied with blood-vessels. A legion of other characters, some of similarity, some of difference, between dog and fish might be enumerated, but enough has been said to show that, different as dog and fish are, they do resemble one another in funda-

mental points of structure; they belong in fact to the same style of architecture.

Now, consider the lobster. To begin with, it has a hard outside armour (often but erroneously called its shell), but neither true hair nor scales. Break open the armour, and you find no bones inside; no skull, no vertebral column. The foremost end of the lobster may be called its head, but how different to the head of the dog or fish! In the first place it is fused with, and can scarcely be distinguished from, the breast or thoracic region. You look in vain for a nose, an olfactory organ. There are two pairs of long jointed feelers borne in front of the head region, and these have numerous bristle-like structures, some of which are considered to serve as olfactory organs, but how different are they from the similarly named organs in dog and fish! The "ear" or auditory organ of the lobster does not lie behind the eyes, but is placed on the basal joint of the first pair of feelers, and is not at all like our ear. The eyes of the lobster have no eye-ball, are placed on a pair of movable stalks, and each is composed of a number of minute facets, very strikingly different from the arrangement of the dog's or fish's eye. The jaws of the lobster do not work up and down, but from side to side; there are several pairs of them, and a little study convinces us that they are nothing more than so many modified pairs of limbs. The lobster walks and swims. It walks by four pairs of jointed legs, in front of which a quite similar pair of limbs is modified to form the great nippers or claws. The posterior region of its body is composed of hard rings, which move on one another. On the under surface of these rings are as many pairs of little limbs used in swimming, the last pair being large, expanded, and forming with the last joint of the body, a posterior expansion used in vigorous swimming movements. Lastly, we find that there is no skull with its enclosed brain in the lobster, and no vertebral column and spinal cord. There is a little nervous mass in front of the mouth, but posteriorly the nerve cord is on the lower instead of on the upper side of the body. The lobster does breathe water by structures called gills, but these are quite unlike the gills of the fish, and are simply bottle-brush-like appendages borne on the body-wall or on some of the legs, and covered over by a fold of the thoracic region of the body-wall. In so far as the jaws, the gills,

and the limbs of the lobster perform the same kinds of functions as in the fish, they may be said to resemble one another. But the resemblance is only one of use and function, not of form, and organs which perform similar functions whilst differing in plan in different animals are said to be *analogous*.

On the other hand, the eyes, skull, backbone, and numerous other parts of the dog and fish clearly resemble one another in plan of structure. Such organs are said to be *homologous*.

It is most important that the student should learn to distinguish between organs which are merely analogous and those which are homologous. Comparative anatomy is largely concerned in establishing homologies between organs which often differ considerably from one another in superficial aspect and in function. In these days we consider organs to be homologous when we can produce evidence to show that they are modifications of some pre-existing organ belonging to a remote ancestor from which all the animals possessing the organs in question have descended. The nature of this evidence, and the reasoning which enables us to assert that the identity in the architectural plan of certain animals is due to their having inherited their leading features from a common ancestor, whilst varying the details in an almost infinite degree, will become apparent in the course of this work.

We must now pass to the more detailed consideration of a single animal type, and learn from it what is the structure of the organs about which we have been talking, and what relative positions they hold to one another. As we are more familiar with the general structure of our own bodies than that of other animals we should do best if we took the human subject as a type; but the study of human anatomy is in many ways inconvenient, and we shall take as our type the common frog, an animal easily obtained, of a size convenient for dissection and sufficiently like the human subject to enable us to learn all the lessons necessary for the elementary comprehension of our subject.

Let it be understood here that the student will make no progress in the study of comparative anatomy unless books and lectures are supplemented by thorough painstaking practical work. No words that ever were spoken or written, no drawings or diagrams, however artistic or simple, can ever bring home to the mind the structure of the animal body without

dissection and microscopical study. The student will find full instruction for the detailed examination of the common forms of animal life dealt with in this book in the excellent practical manuals,* published by the late Professor A. Milnes Marshall. As this work is intended to supplement, not to supersede, practical work carried on by aid of these books, attention will be given rather to the lessons which may be learned and the conclusions which may be drawn from anatomical and embryological facts than to the detailed exposition of the facts themselves. The frog, however, being taken as a type of animal structure, will be described in detail.

We must bear in mind, before we embark on our practical studies, that the object of our practical and literary studies in Zoology is to furnish the mind with clear ideas on animal structure and organisation, and to this end our ideas must be arranged in an orderly and methodical fashion. We must accustom ourselves, from the outset, to think of the organs and tissues of the animal body in a definite order, so that they may readily be called up to our minds without haziness or omission. The order in which we shall deal with the anatomical facts exposed by dissection will not necessarily be the same as that in which they are discovered in the course of practical work. In any animal of complex structure the various organs are so interwoven with one another, and in such different manners in different types of organisation, that it is generally necessary to take into account several systems of organs in the course of any piece of dissection. Moreover, it will frequently be necessary to cut away and destroy one organ in order that another may be exposed. Hence the lessons learned from dissection are apt to confuse us at first unless we deal with them in a methodical manner, keeping our attention fixed upon one set of organs at a time, and eventually constructing a plan of that system from the results obtained by our various dissections. But, whilst we deal with organs and systems of organs in a methodical manner, we

* The Frog: an Introduction to Anatomy, Histology and Embryology. By A. Milnes Marshall. Sixth Edition. Edited by G. Herbert Fowler. London: D. Nutt. 1897.

A Junior Course of Practical Zoology. By A. Milnes Marshall and C. Herbert Hurst. Fifth Edition. London: Smith, Elder & Co.

must remember that we do so for the sake of memory and of precision ; we must by no means shut our eyes to the fact that the relations of one system to another, as we discover them in the course of dissection, are of at least as much importance as the plans of those systems considered apart from one another and the rest of the body. Our object, then, is twofold : to get an accurate idea of each system of organs considered by itself, and to form a conception of the manner in which those systems are united together to make up the sum-total of the organisation of the animal in question.

It is perhaps the most convenient plan to consider the different systems of organs in the order in which they make their appearance in the course of development, or, to speak more accurately, according to the germinal layer from which they are developed, for by so doing we shall bring together the results of anatomical and embryological study, and make the one support and illustrate the other. But, as the study of the adult anatomy of a vertebrate type must precede that of its development, we shall begin by describing the organs of the frog in the order in which they are most conveniently studied in the course of dissection.

CHAPTER I

THE COMMON FROG — RANA TEMPORARIA AND RANA ESCULENTA

The frog commonly found in pools and ditches in England is the brown or grass-frog, **Rana temporaria**. A larger form, more abundant on the Continent than in England, is known as the edible frog, **Rana esculenta**. A third species, intermediate between the two, has been distinguished under the name **Rana oxyrhinus**. The differences between these three common species of European frogs are unimportant, and may be neglected at this stage of our studies.

In a frog belonging to any of these species the following **external characters** may be noted without dissection. The body is divisible into two regions, the head and trunk. There is no neck, the head passing without any distinct break into the trunk. There is no tail. Further, we may recognise sides and surfaces which correspond to those of our own bodies and are similarly named. There is an upper surface, corresponding with our back, which we shall call the **dorsal** surface; an under side or **ventral** surface; an anterior end which indicates the direction in which the animal moves, and a posterior end opposite to it. The attachments of the two pairs of limbs mark the right and left sides of the body.

The whole surface of the body is covered by a smooth moist skin of a greenish yellow hue, mottled on the dorsal surface with dark, almost black patches. The ventral surface is generally yellow.

Frogs have the power of varying their colour within certain limits, so that the same specimen may present very different appearances under different circumstances. The changes of colour enable the frog to approximate its colour to that of surrounding objects, and thus to conceal itself in some measure from its enemies. The mechanism by which the changes are effected lies in the structure of the pigment bodies of the skin,

which are under the control of the central nervous system.

The frog differs much from man and all "beasts," from birds, lizards, snakes, tortoises, and fishes, in the fact that its skin is devoid of hair, feathers, or scales, and there are no claws or nails on the toes and fingers. This, however, whilst true of English frogs, does not hold good for all frogs, nor for the class Amphibia to which the frog belongs. The bull-frog, **Ceratophrys**, for example, has flat bony plates in the skin of the dorsal surface.

There are only two median openings on the surface of the body—viz. the mouth, a large slit-like opening situated at the anterior end of the head, and the **anus** or **vent** (more strictly called the **cloacal aperture**) which lies at the hinder end of the trunk, between the hinder legs, and nearer to the dorsal than the ventral surface. There is but one set of paired apertures—viz. the **external nares** or **nostrils**, a pair of small holes placed upon the snout at the anterior end of the head. A bristle passed through one of the nostrils will be found to pass into the cavity of the mouth by an **internal nostril**. On either side of the head is an eye, which has an eyeball, a coloured portion, or **iris**, and a pupil, as in ourselves. Each eye is protected by two eyelids, of which the upper is thick, pigmented like the rest of the skin, and nearly immovable; the lower is thin, semi-transparent, and freely movable.

Just behind the eye, on either side of the head, is a patch of dark colour, in the middle of which a circular membranous area, bounded by a firm, somewhat raised, ring, can be seen. This is the **tympanic membrane**, or drum of the ear. The frog has no external valve of the ear as have man and beasts, nor has it a passage leading down from the exterior to the ear-drum; the latter is on the surface.

The frog's limbs have a general correspondence with our own, as may be seen at a glance. The front limb or arm is divisible into an upper-arm, technically called the **brachium**, a fore-arm or **ante-brachium**, and a hand or **manus**. The wrist, or **carpus**, is hardly distinguishable externally, but we shall learn more of it when we study the skeleton.

The hind limb comprises a thigh or **femur**, a leg or **crus**, a much elongated ankle or **tarsus**, and a foot or **pes**.

On the hand there are four fingers or digits corresponding

to the four fingers of our own hand. A rudiment of a thumb is present, but it is very small and hidden under the skin. Anatomists count the fingers from thumb to little finger, and sometimes distinguish them by the following names: 1. Pollex, 2. Index, 3. Medius, 4. Annularis, 5. Minimus. In the male frog, the index develops a rough, cushion-like swelling in the breeding season. The fingers of the frog are not webbed. Though the foot has only five apparent toes a close inspection reveals the presence of six. The first, counting from the inner side, is extremely small, and almost hidden beneath the skin. It is a moot point whether it should be regarded as the representative of the great toe or **hallux** of man, or whether it should be regarded as an accessory toe, not represented in man. It is usual to consider the toe next to it, the shortest of the remaining five, as the great toe. Of the five apparent toes the fourth is the longest: they are united by a membranous expansion, and are said to be webbed.

The frog's mouth is furnished with distinct jaws; the upper jaw is a forward continuation of the head, and is not independently movable; the lower jaw is hinged on to the posterior region of the head, and is freely movable in a vertical direction. Jaws of this kind, opening vertically, are only found in **vertebrates**—that is, in animals which have a back-bone, and in them only in the division (which comprises nearly the whole group) known as the **Gnathostomata**. The mouth is furnished with fine pointed teeth arranged in a single row on the edges of the upper jaw, and there are also two small patches of teeth on the fore-part of the roof of the mouth, called **vomerine** teeth. There are no teeth on the lower jaw. The toad, so like the frog in most respects, has no marginal teeth on the upper jaw. On opening the jaws the wide **buccal cavity** is seen, which narrows posteriorly to form the gullet or **œsophagus**. Notice (1) the **posterior nares**, to the outside of and in front of the patches of vomerine teeth; (2) the **Eustachian tubes**, a pair of relatively large apertures, one on each side of the hinder part of the buccal cavity: each leads into a cavity, the **tympanic cavity**, which is closed externally by the tympanic membrane: (3) the **glottis**, a slit-like aperture on the floor of the hinder part of the buccal cavity: it leads through a short **larynx** into the lungs; (4) the prominences on the roof of the buccal cavity,

formed by the projection of the lower sides of the eyeballs; (5) the **tongue**, thin and fleshy, attached to the front part of the floor of the mouth, its free end is "forked," and projects backward towards the throat.

Whilst there is a general correspondence between the mouth and buccal cavity of the frog and our own, there are considerable differences, of which the most important are, the absence in the frog of mobile lips; the marginal teeth of the upper jaw correspond in position to ours, but they are more numerous, are not implanted in sockets, are all alike simple and pointed, instead of being of various shapes as ours are. The vomerine teeth of the frog have no counterpart in man. The posterior nares, situated right forward in the upper jaw of the frog, are carried backward in man by the formation of the "roof of the mouth" or **hard palate**, followed by a fleshy curtain or **soft palate**, so that they open far back at the entrance to the throat. The hard palate in man also excludes the orbits altogether from the region of the mouth. The tongue of man, fixed at the back of the mouth, with its free end projecting forward, is obviously different from that of the frog.

Already, after an examination of the external features of the frog, we are able to make a comparison of its structure with our own, and to recognise a general correspondence of plan, with numerous differences in detail. We cannot escape from the conclusion that the frog is built on the same principle as ourselves; and yet not a single organ or feature that we have examined is exactly or even nearly the same as it is in man. The science of comparative anatomy takes account both of the resemblances and the differences, and embodies the results of its comparison in a system of classification. The frog, because of the resemblances which we have already noted, and many others of greater importance relating to the internal organs, is placed in the **phylum** vertebrata along with fishes, reptiles, birds, and beasts. But the differences compel us to place it far apart from man in a **class** comprising many other animals such as newts and salamanders: in this class, **Amphibia**, the component members resemble one another in all their more important characters, and differ only in those which are relatively unimportant. But comparative anatomy does more than this. It seeks to give an explanation of the resemblances and of the differences, and it finds the explanation in the

doctrine of the common descent of all the animals composing a phylum from an ancestor which embodied all the fundamental peculiarities of structure which distinguish the phylum from all other phyla. But the justification of this doctrine can only be understood after a considerable study of the internal as well as the external anatomy of different kinds of animals.

Turning now to the internal anatomy of the frog, we will begin by a general consideration of the principal organs and systems of organs, without at first going into very exact details concerning them.

The body, we have seen, is covered by a smooth moist skin or integument, which lies rather loosely so that it can easily be pinched up in folds without including the underlying parts. Cutting through the skin with knife or scissors we find that it is attached by sheets of a white glistening substance to the flesh beneath. This white substance is called **connective tissue**, and it does not tie down the skin evenly in all places, but only along certain lines, so that large spaces are left between skin and flesh which are filled with a colourless fluid called **lymph**. The most important of these spaces, known as lymph-sacs, are (1) a dorsal lymph-sac, extending over nearly the whole of the dorsal surface of the head and trunk, and separated on either side by a septum from (2) the lateral lymph-sacs, which occupy the flanks of the animal; (3) the ventral lymph-sac, a large triangular sac extending from the breast region over the abdomen on the ventral surface; (4) the pectoral lymph-sac, lying over the region of the breast; and (5) the submaxillary lymph-sac, occupying the ventral surface of the head and throat. There are other lymph-sacs on the fore and hind limbs. These large sacs are connected with other lymph-spaces lying between the muscles and organs of the body, and the fluid which they contain is eventually carried into the blood stream.

After the skin has been stripped off, the body is seen to be covered with muscle, commonly called the "flesh" of the animal. The use and mode of contraction of the muscles has already been explained (p. 6). We need only notice here that the muscles which are exposed on the removal of the skin belong to the system known as voluntary muscles; by their means all the voluntary movements of the body are effected. Over the back, flanks, and belly the muscles have, for the most

part, the form of flat sheets of fleshy tissue, composed of numerous fibres which either run parallel with one another or diverge outwards in a fan-shaped manner from the point of attachment to the line of insertion (*e.g.* the muscles of the breast). In the limbs the muscles are more rounded or spindled-shaped, their component fibres being gathered into bundles which terminate at each end in a tendon. The general character of a muscle may most conveniently be studied in the calf-muscle or **gastrocnemius** of the frog. This muscle lies on the inner surface (that surface which in man would be hindermost) of the leg. It is stout and spindle-shaped, tapering towards either extremity, but most markedly towards the lower end, where it passes into a stout glistening white tendon, the **tendo Achillis**. It is attached at the upper end by a broad tendon to the bone of the thigh, and to the upper end of the bone of the leg. The tendon at the lower end passes round the place where the heel would be, if such a structure were present in the frog, and is continuous with a broad sheet of connective tissue spread over the sole of the foot. Such a sheet of connective tissue serving for the attachment of muscle or tendon is called an **aponeurosis**, and this particular one is known as the **aponeurosis plantaris**. The gastrocnemius muscle by its contraction pulls upon the back of the ankle and the sole of the foot, and tends to bring the foot and ankle in a line with the leg. The bones to which the upper end of the muscle is attached are not moved by its contraction, and this fixed end of the muscle is called its **origin**. The opposite end, which is moved when it contracts, is called its **insertion**. Most of the voluntary muscles are attached, at one of their ends at least, to bones. The bones of an animal constitute its skeleton, and afford a system of levers actuated by the muscles: they also form a solid framework which supports and protects some of the organs.

We have already been able to recognise the fact that the skeleton of the frog is internal, in this respect resembling our own, and differing from the skeleton of such animals as lobsters and insects, which have their skeleton on the outside.

In the frog's skeleton we may recognise two main parts, an **axial** and an **appendicular** skeleton. There is also a **branchial** skeleton well developed in the tadpole, but reduced and of minor importance in the adult frog. The axial skeleton, so

named because it lies along the main longitudinal axis of the body, consists of the **skull** and the **vertebral column**. We will first consider the vertebral column. It is made up of ten pieces, nine being peculiarly shaped rings of bone called vertebrae, the tenth being a long rod-shaped piece called the **urostyle**; it is the representative of a number of fused vertebrae.

A typical vertebra (the fourth or fifth in the frog will serve as a type) consists of a short cylinder of bone called the body or **centrum**, on the top of which is placed a flat bony **arch** in such wise that the centrum below and the arch above enclose a space through which in life the spinal marrow passes; hence it is called the **neural arch**. The bodies of the vertebrae are jointed together, and the arches are also connected by sliding joints called **zygapophyses** (Greek ζυγόν, a yoke; ἀπόφυσις, a process), and so the nine arches enclose a canal, the **neural canal**, or canal of the spinal cord. Examining the vertebra more closely it will be seen that its posterior end is a rounded knob covered with smooth white cartilage, while its anterior end presents a concavity lined with cartilage. The bodies of the vertebrae are, in fact, connected by ball and socket joints, and the ball is on the hinder, the socket on the anterior, face of each vertebra, excepting the first, eighth, and ninth. The centrum of the eighth vertebra is concave at both ends; that of the ninth is convex anteriorly, and posteriorly it has two small rounded processes for articulation with the urostyle. The first vertebra will be more particularly described further on. A vertebral centrum which is concave in front and convex behind is called **procœlous**; one which is, like the eighth vertebra, concave both anteriorly and posteriorly, is called **amphicœlous**; and one which is convex in front and concave behind (not represented in the frog) is called **opisthocœlous** (προ, in front of; ὄπισθε, behind; ἀμφί, on both sides; κοῖλος, hollow). If the centrum of a vertebra is sawn across the middle it will be found to contain a central cavity filled with a peculiar tissue. This is the remnant of the **notochord** or **chorda dorsalis**, the primitive skeletal rod which formed the backbone of the embryo, and has been replaced by bone. A notochord is the first part of the skeleton to be formed in the embryos of all Vertebrates. In some it is persistent throughout life; in others it is surrounded by, or replaced by, cartilage or bone, but traces,

larger or smaller, of it are generally to be found. A word of warning is here necessary. Since the vertebral column is sometimes called the spinal column, or simply the spine, and since the column of nervous tissue which is enclosed by the arches of the vertebral column is generally called the spinal cord, the beginner is apt to confuse the notochord with the spinal cord. It must be clearly understood that the nervous structure, the spinal cord, lies **above** and not inside the centrum, and that it is the notochord, the embryonic structure, which occupies the cavity when present in the vertebral centrum.

The arch of the vertebra (fourth or fifth) consists of a flat dorsal expansion, united on either side to the centrum by a narrow pedicle. When the vertebrae are jointed together in the natural position, spaces are left between the pedicles of successive vertebral arches through which, in life, the spinal nerves emerge from the neural canal. From each side of every arch a stoutish bony piece, the **transverse process**, projects outwards.

Each arch is yoked to its fellows in front and behind by a pair of articular processes, already referred to as **zygapophyses**. These processes project forward and backward from the outer angles of the arch. Their articular surfaces are flat, and it is an invariable rule in the Vertebrata that the articular faces of the anterior zygapophyses look upward or inward, those of the posterior zygapophyses downward or outward. Thus one can tell the anterior end of a single vertebra by mere inspection of the zygapophyses. In addition to the processes already detailed, each arch has a ridge running along its median dorsal line. This is called the **neural spine**, and it is much smaller in the frog than in many other Vertebrata. The transverse processes do not all stand at right angles to the axis of the vertebral column, but point in various directions. There is no transverse process in the first vertebra; those of the second are directed downward and forward; those of the third very slightly backward; those of the fourth much more backward; those of the fifth, sixth, seventh, and eighth stand nearly straight out; and those of the ninth are very large and stout and point very markedly backward. Each transverse process has a little tip of cartilage called an epiphysis.

The first or **atlas vertebra** differs markedly from the rest.

It has a very thin centrum, much compressed from above downward, and a wide ring-like arch. Posteriorly the centrum bears an articular head, but anteriorly, instead of a single concavity, there are two oval, concave, articular surfaces, separated from one another by a median projection. These concavities receive the occipital condyles of the skull. There are no transverse processes. The **urostyle** is nearly as long as the rest of the vertebral column. It is a rod-like bone with a ridge on the dorsal surface, which is high and thick in front, and becomes lower and thinner behind, eventually disappearing altogether. The front end of the urostyle is thick and broad, and has two concavities for articulation with the two posterior prominences of the ninth vertebra. The anterior portion of the ridge of the urostyle is hollow, and in life contains a prolongation of the spinal cord known as the **filum terminale**. The anterior end of the urostyle presents an opening on either side through which nerves pass outward from the spinal cord ; and just in front of each opening a small process may generally be found which represents the transverse process of an ordinary vertebra. The lateral openings represent the spaces which are left between the pedicles of the arches of the successive vertebrae of the column, and similarly serve for the transmission of the spinal nerves. The vertebrae are bound together by ligaments, and the whole column is capable of a certain amount of flexion, in virtue of the articulations of the centra and arches of its component vertebræ. The column, especially its neural and transverse processes, serves for the attachment of some of the most important muscles of the trunk.

The skull is articulated to the first vertebra by two prominences, known as the **occipital condyles**, which fit into its two concavities.

The skulls of all the **craniate** vertebrates (by which we mean those vertebrate animals which have a distinct head) present certain features in common, and though that of the frog is peculiar in some respects, it is fairly illustrative of the fundamental features of all skulls.

A skull comprises the following parts: (1.) A **brain case** or **cranium** proper; this is a cartilaginous or bony, or, as in the frog, partly cartilaginous, partly bony, box, which contains the brain. At the back of the brain-case is a large aperture, the **foramen**

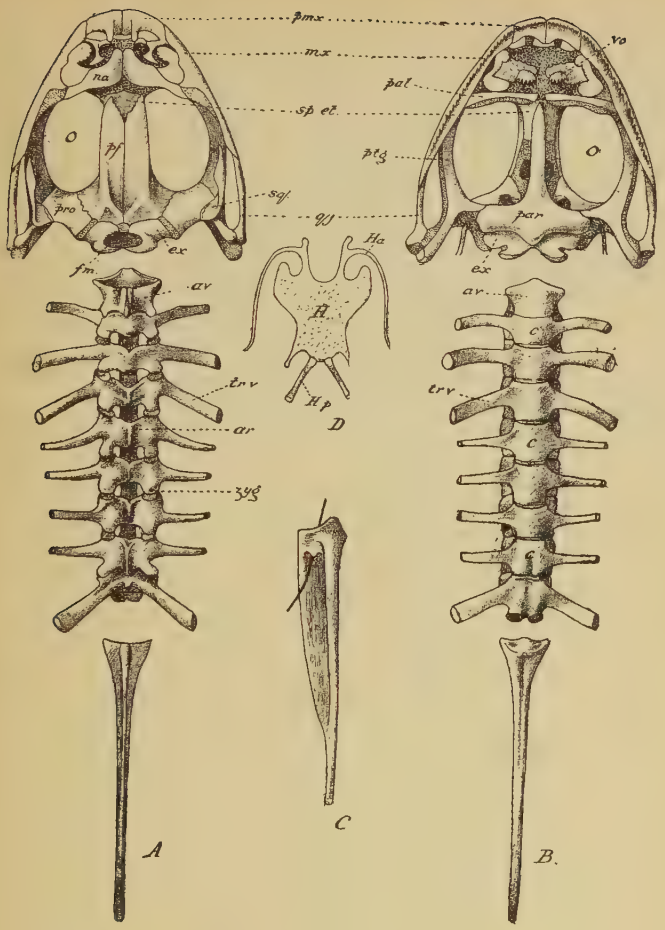

Fig. 1.

A, The skull and vertebral column of the Frog, viewed from the dorsal surface. *B*, The same from the ventral surface. *C*, Lateral view of the urostyle; a bristle is passed through the foramen for the tenth spinal nerve. *D*, The branchial skeleton of the Frog. (All the figures after Ecker.) *O*, orbital fossa; *pmx*, premaxilla; *mx*, maxilla; *q-j*, quadrato-jugal; *na*, nasal; *pf*, parieto frontal; *ex*, ex-occipital; *fm*, foramen magnum; *pro*, pro-otic; *sq*, squamosal; *sp. et*, sphenethmoid; *par*, parasphenoid; *pal*, palatine; *vo*, vomer; *ptg*, pterygoid; *av*, atlas vertebra; *c*, centrum; *ar*, neural arch; *zyg*, zygapophysis; *trv*, transverse process; *ur*, urostyle; *H*, body of the hyoid; *Ha*, anterior cornu; *Hp*, posterior cornu of the hyoid.

magnum, by means of which the spinal cord passes into the brain. (2.) The **sense capsules**, of which there are three pairs. The **olfactory capsules**, which contain the organs of smell, are situated anteriorly ; the **auditory** or **otic capsules**, containing the organs of hearing, are situated one on each side of the posterior region of the cranium. Both the auditory and olfactory capsules are firmly united to, and continuous with, the cranium. The **optic** capsules, comprising the organs of sight, are never united to the cranium, but profoundly modify that part of the skull in which they lie. (3.) **The jaws**, present in nearly all craniate vertebrates, comprise an upper and a lower jaw. The latter is always articulated to the skull, and falls away from it in the dried skeleton (except in the badger and sea-otter) ; the upper jaw in the majority of vertebrata is firmly fastened to the cranium, and appears to form part of it.

The frog's head is large, flat, triangular in shape, with the blunt apex forming the snout. But the cranium is relatively small, the large size of the head being due to the wide sweep of the jaw-bones and the large size of the cavities for the eyes.

In the tadpole the brain case is entirely composed of cartilage, but in the adult frog certain regions of the cartilaginous case become ossified—turned into bone—but the greater part remains cartilaginous throughout life.

On either side of the great hole—the foramen magnum—at the back of the cranium, is an ossification known as the **ex-occipital**. The ex-occipitals are separated from one another by a cartilaginous piece above and below in the middle line, but elsewhere form the border of the foramen magnum, and they bear two cartilaginous articular heads, the occipital condyles, for articulation with the atlas vertebra.

The roof, the sides, and the floor of the middle part of the cranium are cartilaginous, but anteriorly it is completed by a single bone, shaped somewhat like a dice box, one cavity of which, the posterior, lodges the fore part of the brain ; the other, divided into two by a median vertical partition, affords a passage for the nerves of smell, and lodges part of the olfactory organs. This bone, the **sphenethmoid**, is peculiar to Batrachia.

The ex-occipitals and sphenethmoid are the only ossifications of the cranium proper, but there is a pair of ossifications in the ear-capsules which are continuous with, and scarcely to be

differentiated from, the cranial box. The ear-capsules are placed one on either side of the posterior region of the cranium, where they form prominent projections. The anterior and lower face of each projection presents an ossification known as the **pro-otic** bone.

Anteriorly, the cartilage of the cranium is continued directly into the cartilage of the olfactory chambers or nose; so we see that the central portion of the frog's skull is a cartilaginous brain-box, with which the cartilaginous olfactory capsules are continuous in front, the auditory capsules at the side and behind; and the cartilage is replaced by bone in the ex-occipital, the sphenethmoid, and the pro-otic regions. But the brain-box and sense organs are further protected by bones above and below, which are not ossifications in cartilage, but are formed in membrane as sub-dermal ossifications in the integument covering the head. These bones over- or underlie the cartilaginous cranium, and can easily be stripped off it, whereas the ossifications in cartilage cannot be stripped off. Above, running from the occipital or posterior region of the skull as far forward as the sphenethmoid, is a pair of bones called the **fronto-parietals**. In front of these a pair of triangular **nasals** roof over the cartilage of the chambers of the nose. Below, the whole floor of the cranium is protected by a large dagger-shaped bone, the cross-pieces of the handle reaching beneath the auditory capsules. This is the **parasphenoid**. The floor of the olfactory region is occupied by a pair of small irregularly-shaped bones, the **vomers**, which bear each a patch of teeth.

The broad triangular skull is completed by the jaws and the suspensory apparatus by which the jaws are attached to the cranium. The gape of the upper jaw is bordered on either side by a **pre-maxilla** in front and a slender **maxilla** behind, both bearing teeth. These two bones are ossifications in the sub-dermal membrane and therefore are membrane bones. The maxilla is attached to the cranium before and behind by bony and cartilaginous struts. From the **ethmoid** region of the skull, just in front of the sphenethmoid bone, a bar of cartilage runs out on either side. This bar is covered below by a slender bone, the **palatine**. It is usual to reckon the palatine among the "cartilage bones" of the skull because in most animals it is

preformed in cartilage. But, as a matter of fact, in the frog it is a membrane bone, which largely or wholly replaces the ossification in cartilage. The same is the case with a large three-headed bone, the **pterygoid**, which reaches from the point where the palatine unites with the maxilla to the auditory process of the skull, and gives off outward and backward a process towards the articular surface for the lower jaw. This posterior limit of the pterygoid lies beneath a rod of cartilage which extends from the pro-otic region outward and backward, and is known as the **quadrate** cartilage. Externally it presents a concave articular surface, the **glenoid cavity** for the lower jaw; it is covered below by the process of the pterygoid as described, and above by a T-shaped bone, the **squamosal**. Finally, the posterior end of the maxilla is connected with the outer end of the quadrate cartilage by a small splint-shaped bone, the **quadrato-jugal**. It should be noticed that the palatine and pterygoid, with the cartilage which overlies them, form the front and exterior borders of a cavity which is completed internally and posteriorly by the cranium and auditory process. In this cavity the eye is lodged, and it is known as the **orbital cavity**, or, more shortly, the **orbit**. It is open below, so that the eyeballs are only separated from the mouth-cavity by the integuments lining the latter and by a thin sheet of muscle. The **lower jaw** or **mandible** consists of two bars of cartilage, one on each side, frequently known as **Meckel's cartilages**, united in the middle line in front by ligament. Each cartilage ends in front in a little ossification, the **mento-Meckelian** (cartilage-bone), and is ensheathed by two membrane bones, the **angulo-splenial**, inside and below, and the **dentary** covering the upper and outer sides of the anterior half of Meckel's cartilage. The last named widens out behind and forms the articular head which fits into the glenoid cavity of the suspensorium.

The Branchial skeleton is very much reduced in the adult frog, and comprises what is known as the **hyoid** apparatus. This lies on the ventral surface of the throat and consists of a broad thin cartilaginous plate, the **body of the hyoid**, from which processes are given off anteriorly and posteriorly. The anterior processes or **cornua** are cartilaginous and run first forward and then upward and backward as two slender curved cartilaginous rods which are united with the cartilage

of the auditory region. The **posterior cornua** are bony rods which diverge from one another and enclose between them the larynx.

The frog has no ribs, unless the little cartilaginous

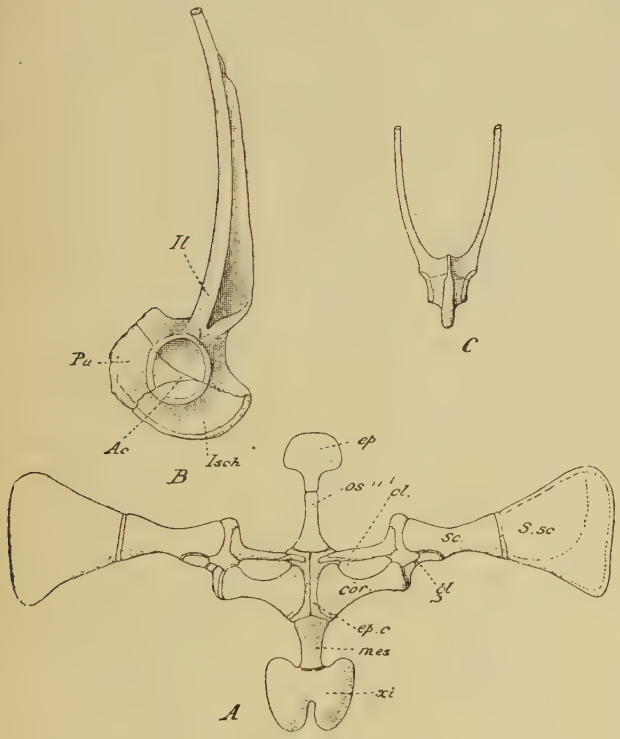

Fig. 2.

A, The shoulder girdle of the Frog; the scapula and suprascapula are turned outwards. *ep*, episternum; *os*, omosternum; *ep*, *c*, epicoracoids; *mes*, mesosternum; *xi*, xiphisternum; *s*, *sc*, suprascapula; *sc*, scapula; *gl*, glenoid cavity; *cor*, coracoid; *cl*, clavicle. *B*, The pelvic girdle of the Frog, viewed from the side. *Il*, ilium; *Isch*, Ischium; *Pu*, cartilaginous pubis; *Ac*, acetabulum. *C*, The pelvic girdle of the Frog, viewed from below. (All the figures after Ecker.)

epiphyses at the ends of the transverse processes of the vertebrae are to be considered as rudiments of such. But

there is a distinct **sternum** or breast-bone with which the lower ends of the shoulder-girdle articulate.

In the mid-ventral line of the breast there lies anteriorly a flat circular plate of cartilage called the **episternum**. Posterior to this is a bony rod, the **omosternum**. This is succeeded by a pair of cartilaginous strips, the **epicoracoids**, which belong to the shoulder-girdle; and these again are succeeded by the **mesosternum**, a rod of cartilage ensheathed in bone; and hindmost of all the **xiphisternum**, a flat plate of cartilage, somewhat heart-shaped, with a bifid apex.

The shoulder-girdle proper is to be thought of as two half-rings of bone and cartilage which encircle the fore-part of the body; they are united below in the sternum but are separate above. Each half-ring is divided by an articular cavity, the **glenoid**, into an upper or **scapular** and a lower or **coracoid** moiety. The scapular moiety comprises an upper expanded portion formed of calcified cartilage, the **suprascapula**, and a lower bony portion, the **scapula**. In the coracoid moiety we distinguish a **coracoid**, a stout bony rod, expanded at its two ends and joined to its fellow of the opposite side by the intervention of the epicoracoid cartilages already mentioned. In front of the coracoid a rod of cartilage known as the **pre-coracoid** connects the scapula with the anterior ends of the epicoracoids, and this rod is ensheathed by a splint-like bone generally described as the **clavicle** or **collar-bone**

In the fore-limb there is one bone, the **humerus**, in the upper arm. It has a shaft and two articular surfaces, one at each end. That of the upper or proximal extremity of the bone is called the head, and fits into the glenoid cavity of the shoulder-girdle. The distal extremity has a rounded knob, internal to which is a small flat articulating surface, the **trochlea**, placed upon a little eminence called the **internal condyle**. There is a similar **external condyle** on the outer side of the articular process.

The fore-arm has two bones, the **radius** and the **ulna**, but they are firmly and immovably united together throughout their length so as to form one bone, the **radio-ulna**. The upper end of the double bone has a large concavity for articulation with the humerus, beyond which a hook-shaped process, the **olecranon**, projects from the ulnar component of the bone. At its distal end the radio-ulnar bears two articular surfaces

belonging to the ulnar and radial components respectively. In ourselves the ulna and radius are separate; the former takes the main articulation with the humerus, the latter the main articulation with the wrist. The radius can be crossed over the ulna, carrying the wrist and hand with it, and thus we are able to turn our hands palm upwards when the bones are

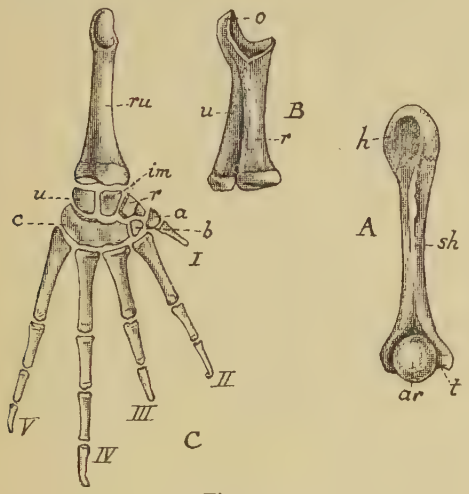

Fig. 3.

A, Humerus of a female Frog, seen from below. *h*, head; *sh*, shaft; *ar*, distal articular knob; *t*, trochlea. *B*, Radio-ulna of the right side. *o*, olecranon; *r*, radius; *u*, ulna. *C*, Forearm and hand of the right side, seen from above. *ru*, radio-ulna; *I—V*, the five digits; *r*, radiale; *im*, intermedium; *u*, ulnare; *a*, first distal carpal bone; *b*, second distal; *c*, third distal. (All the figures after Ecker.)

parallel (supination), or palm downwards when the bones are crossed (pronation). In the frog the radius and ulna, though fused together, are fixed half-way towards pronation.

The wrist of the frog comprises six little **carpal** bones arranged in two rows. In the proximal row there are three bones: one corresponding to the radius, which we call the **radiale**; one corresponding to the ulna, the **ulnare**, and one between the two, the **intermedium**. In the distal row we find,

beginning on the radial or thumb side, two small bones corresponding with the rudimentary thumb and the second digit, these we call distals 1 and 2 ; and there is a much larger crescentic bone which represents distals 3, 4, and 5 fused together. The hand consists of a set of five proximal bones joined on to the wrist ; these are the **metacarpals**, and the first is very small. To the metacarpals succeed the **phalanges**, forming the fingers. The two longest fingers, IV and V, have each three phalanges ; the third and second have only two. The thumb is only represented by the metacarpal.

The hind-limb, like the front, is swung on the body by means of a girdle, the **pelvic** girdle. There is this important difference between the pectoral and pelvic girdles, that whereas the former is not directly attached to the vertebral column, and is only kept in its place by muscles, the latter is articulated to the transverse processes of one or more vertebrae, known as the **sacral** vertebrae. In the frog there is one sacral vertebra, the ninth, and to its broad and long transverse processes a pair of long and rather slender bones, the **ilia**, are articulated. Each ilium curves downward and inward so as to approach its fellow of the opposite side, and, expanding into a broad plate posteriorly, it is firmly bound to the similar expansion of its fellow by ligament. Each ilium has a crest on its upper edge, and the external surface of its posterior expansion is occupied by the half of a deep articular concavity, the **acetabulum**, into which the head of the thigh-bone fits. The acetabulum is completed by an irregularly-shaped bone, the **ischium**, above and behind, and a wedge-shaped piece of cartilage, the **pubis**, in front and below. Both ischium and pubis are placed back to back with their fellows of the opposite side ; and are firmly united to them by ligament. The whole pelvis of the frog has thus somewhat the shape of the "merry-thought" of a bird (but the latter has nothing to do with the pelvis) and is abnormal in structure. Each half of a typical pelvic girdle consists of an ilium above united to one or more sacral vertebrae. The ilium constitutes the dorsal moiety of the girdle, and is analogous with the scapula in the pectoral girdle. The ventral moiety consists of an ischium, which inclines backward, and a pubis, which inclines forward. The ischia and pubes of opposite sides commonly meet, and are joined together in the mid-ventral line; the points

of union are known as the ischial and pubic **symphyses**. The dorsal moiety is separated from the ventral by the acetabulum, just as in the pectoral girdle the scapular half is divided from the coracoid half by the glenoid, and all three bones, ilium, ischium, and pubis enter into the composition of the acetabulum. The peculiarity of the frog's pelvis consists in the great relative length of the ilia, the reduction in size of the ischia and pubes, and the flattening and approximation of the members in the region of the acetabulum.

The thigh-bone or **femur** is a long cylindrical bone with a slight S-shaped curvature. The shaft is ossified; the upper extremity has a rounded cartilaginous articular head placed directly on the shaft; and the extremity also has a rounded cartilaginous surface for articulation with the leg-bone.

The crus of those vertebrates which have limbs with five fingers or toes has typically two bones. Both are present in the frog, but so firmly and intimately are they fused together that they seem to form a single bone, the **os cruris**. But, if it is cut across the middle, two cavities are seen, showing that the bone is double; and its double nature is further expressed by longitudinal grooves on the surface. We shall therefore call it the **tibio-fibula**. Its upper end has a grooved articular surface for the femur, and its lower extremity a transversely elongated surface for articulation with the ankle.

The ankle of the frog is peculiar. Its proximal portion consists of two rather long bones, separated from one another in the middle; but their extremities approach one another and are bound together proximally and distally by cartilaginous articular epiphyses. These two bones represent the proximal row of the ankle or tarsal bones, and correspond to the heel-bone (**calcaneum**) and ankle-bone (**astragalus**) in man. The further row of tarsals is very much reduced, consisting of two tiny pieces of calcified cartilage. One, a flat piece, lies between the common epiphysis of the astragalus and calcaneum and the metatarsal bones of the foot, and is generally considered to correspond to the **cuboid** of human anatomy. The other piece is a mere nodule on the inner or astragalar side, and is compared with the **navicular** bone of human anatomy. The foot has six toes. The first is minute with a very small proximal piece articulating with the navicular,

and probably representative of the metatarsal. This is succeeded by a flat crescentic piece representing a phalanx. The first toe is generally called a supplemental toe, and, as we have already seen, the innermost of the longer toes is usually reckoned as the hallux or great toe. There are five fairly long **metatarsals** in the foot, and to these succeed the

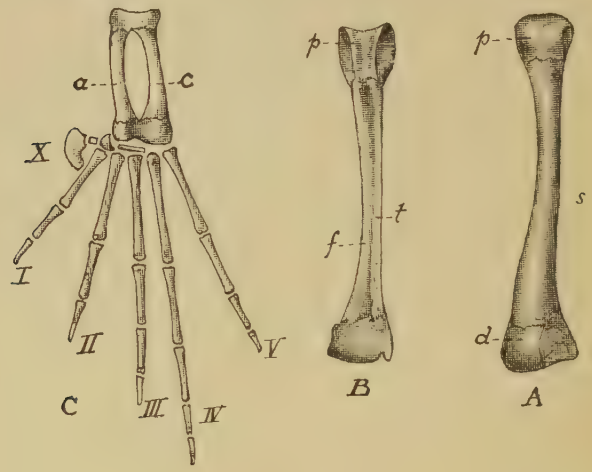

Fig. 4.

A, Femur of the Frog. *p*, proximal; *d*, distal articulating surfaces; *s*, shaft. *B*, Tibio-fibula, seen from below. *p*, proximal; *d*, distal articulating surfaces; *t*, tibial half of the bone separated by a groove from *f*, the fibular half. *C*, The right ankle and foot of the Frog, seen from below. This figure is drawn to a smaller scale than *A* and *B*. *a*, astragalus; *c*, calcaneum; *I*—*V*, the five principal digits; *X*, the minute accessory digit. (All the figures after Ecker.)

phalanges of the toes. The first and second toes have two phalanges, the third three, the fourth four, and the fifth three.

It is obvious that the fore and hind limbs are built on essentially the same plan. The humerus of the arm has its analogue in the femur of the leg. The radius and ulna are represented respectively by the tibia and fibula in the leg. The wrist corresponds to the ankle, and the bones of hand and foot are very similar. Paired structures, which are repeated in this way, are said to be serially homologous, but

we shall find better examples of serial homology among the Invertebrates.

The limbs of the frog have undergone considerable modification in connection with its swimming and leaping habits; the limbs of man are more typical, but the best examples of typical limbs are to be found among the long-tailed amphibia and the reptiles.

When we say that a limb or any other organ is *typical*, we mean that it conforms to a pattern which we recognise as being the fundamental standard to which all the limbs belonging to members of the group may be referred. This fundamental pattern does not always exist in Nature, though it does in the case of limbs. It may be, in the case of other organs, an abstraction, a design, of which we form the idea after the comparison of a great number of limbs, all resembling one another in some particulars, but differing from one another in this character and in that. In the case of limbs, the differences are chiefly in the suppression or fusion of parts: it is rare that there is an addition of parts as in the case of the supplemental toe of the frog's foot.

The examination of a large number of cases leads to the recognition of the following plan of structure for the limbs of amphibia, reptiles, birds, and beasts; those vertebrata which we consequently class together as Pentadactyla.

Suppose the animal to be placed on the table, belly downward, and its head pointing away from the observer; a straight line drawn from the mouth to the tip of the tail divides it into equal and symmetrical right and left halves. This line is called the principal axis of the body, and as the halves into which it divides the animal are alike, the animal is called bilaterally symmetrical. The skull and vertebral column coincide with the principal axis, hence we have referred to them as the axial skeleton. Let two lines be drawn at right angles to the principal axis from the points where the limbs are joined on to the body; these will be the two secondary axes. Let us suppose the limbs to be straightened out along the secondary axes, as in the diagram, palms downward. Then we find that the humerus in the arm, and the femur in the leg, correspond with the secondary axes. In the fore-arm the radius lies in front of the secondary axis, and is called pre-axial; the ulna lies behind it, and is called

post-axial. Similarly, in the leg, the tibia is pre-axial, the fibula post-axial. In the wrist we find a proximal row of three bones—**radiale** lying beyond the radius, **ulnare** lying beyond the ulna, and a median bone, the **intermedium**, lying between them. The distal row has five bones, and we begin counting from the pre-axial or radiale side. The thumb, therefore, is

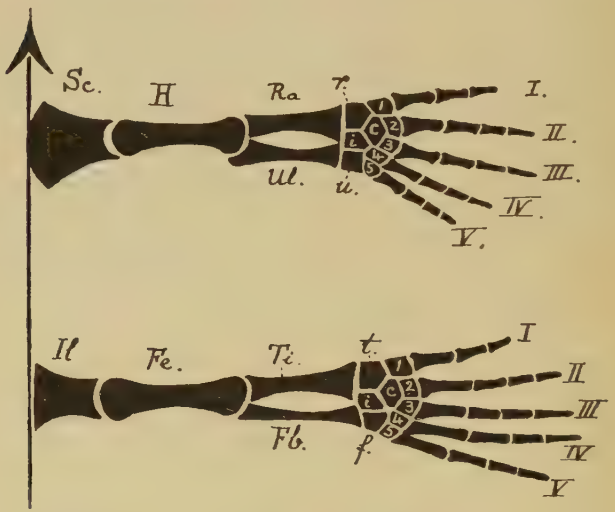

Fig. 5.

Diagram of the typical fore and hind limbs of a pentadactyle vertebrate. The arrow represents the principal axis of the body, the point directed anteriorly. The limbs are represented as stretched straight out at right angles to the principal axis, palms downwards. *Sc*, scapula; *H*, humerus; *Ra*, radius (pre-axial with regard to the secondary axis); *Ul*, ulna (post-axial); *r*, radiale; *u*, ulnare; *i*, intermedium; *c*, centrale; 1, 2, 3, 4, 5, the distal row of five carpals; *I*, *II*, *III*, *IV*, *V*, the five digits; *Il*, ilium; *Fe*, Femur; *Ti*, Tibia (pre-axial); *Fb*, Fibula (post-axial); *t*, tibiale; *f*, fibulare.

on the pre-axial side. Between the proximal and distal row of carpals a **central** bone is wedged in. This condition is realised in the hand of the water-tortoise. In the ankle we similarly find a **tibiale** (pre-axial), a **fibulare** (post-axial), and between them an **intermedium**. There is a **centrale** and a distal row of five bones. This condition is realised in the

foot of the spotted salamander. But in most animals some of the carpal and tarsal bones are fused together, as in the frog. In man we find in the carpus that the radiale, intermedium, and ulnare are present as separate bones, and they are called **scaphoid**, **lunar**, and **cuneiform**, respectively. The centrale is present in the fœtus, but becomes fused with the third bone of the distal row to form the **os magnum**. The first and second bones of the distal row, called the **trapezium** and **trapezoid**, are separate; the fourth and fifth are fused together, and are called the **unciform**. In the foot the tibiale and intermedium are fused to form the **astragalus**, the fibulare forms the **calcaneum**. The centrale remains separate, and is called the **navicular**; the first, second, and third distals are called the **ento-cuneiform**, **meso-cuneiform**, and **ecto-cuneiform**, respectively; the fourth and fifth are fused together to form the **cuboid**. After this explanation the limb bones of the frog should present no difficulty.

CHAPTER II

THE FROG (continued)

We have treated the skeleton of the frog in detail, but for the present we will pass the remainder of its anatomy in somewhat rapid survey, leaving details for further study at a later time.

On making an incision through the muscular sheet which covers the abdomen, we open up a spacious cavity, in which the gut and other organs lie. Extending the cut farther forward, and cutting through and removing the breast-bone, we find that the cavity is prolonged forward into the region of the heart, and that the heart lies in a part of it which is cut off from the abdominal part by a partition formed by the insertion of some of the abdominal muscles on the œsophagus. This cavity is the pleuro-peritoneal cavity, or **cœlom**. It must be noticed that it does not contain blood, and that it is lined by a smooth, glistening, pigmented membrane—the **peritoneum**. Tracing the peritoneum round to the dorsal side, we find that under the vertebral column, in the mid-dorsal line, it is folded ventralward on each side, and the two folds are so closely applied that they form an apparently single sheet of transparent tissue, the **mesentery**, by which the gut is suspended in the cœlom. The other organs which lie in the cœlom—ovaries, liver, etc.—are similarly suspended from the dorsal wall by a reflection of the peritoneal membrane, which passes right round them. It should be clearly understood that the gut and other organs which appear to lie in the cœlom are in reality external to it, being separated from it by the mesenterial fold. This will be clear if we liken the abdomen of the frog to a stout bag with an inner lining representing the peritoneum. The gut, etc., do not lie in the cavity, enclosed by the lining, but are placed between the lining and the outer wall of the bag. The gut lies in a deep fold of the lining which projects into the cavity, and the upper or suspensory limbs of the fold are closely pressed together, and form the mesentery. These

relations are exhibited in the diagram (fig. 6), in which the peritoneum and the mesenterial folds are represented by a broken line. The cœlom, then, is a cavity which contains a fluid, the peritoneal fluid, but not blood; the viscera project into this cavity, but are in all cases separated from it by folds of the peritoneum. The peritoneum, over

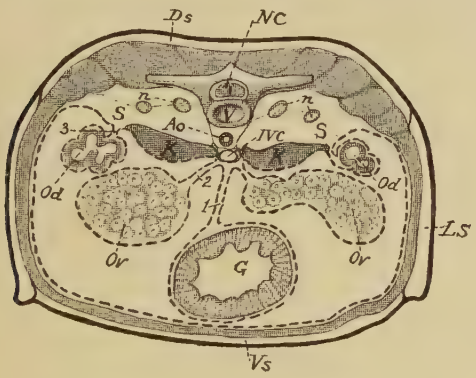

Fig. 6.

Diagrammatic transverse section of the body of a female Frog, taken at the posterior end of the eighth vertebra, to show the relation of the peritoneal membrane, represented by a broken line, to the viscera. *V*, vertebral centrum; *NC*, spinal cord; *n n*, nerves; *S S*, the great dorsal lymph spaces; *Ao*, aorta; *IVC*, inferior vena cava; *K K*, kidneys; *Ov Ov*, ovaries; *Od Od*, oviducts; *G*, gut; *1*, the mesentery, a double fold of peritoneal membrane suspending the gut; *2*, the mesovarium, a similar peritoneal fold suspending the ovary; *3*, the mesometrium, a similar peritoneal fold suspending the oviducts; *Ds*, dorsal subcutaneous lymph space; *LS*, lateral subcutaneous lymph space; *Vs*, ventral subcutaneous lymph space. The skin is represented by a thick black line.

the greater part of the surface of the abdomen, is closely adherent to its muscular walls, except for the mesenterial and other folds referred to. On either side of the kidney, on the dorsal side, it is separate from the muscular walls of the abdomen, leaving a space, which is filled with lymph. The peritoneum in the region of this space is found, on careful microscopical examination, to be perforated by numerous tiny apertures called stomata, putting the cœlom into communica-

tion with the lymph space. This last communicates with the general system of lymph spaces in the body, which, in their turn, communicate, by means of two pairs of small pulsatile vesicles called **lymph hearts**, with the blood system. One pair of lymph hearts lie just behind the transverse processes of the third vertebra, the other pair alongside of the urostyle.

Thus we see that the cœlom, though it does not contain blood, is, in a roundabout way, in communication with the blood-vessels.

The most obvious organ, when the body cavity is opened, is the gut, with its great glandular appendages, the **liver** and **pancreas**. The buccal cavity passes into a wide tube, the gullet or **œsophagus**, which passes straight backwards underneath the vertebral column in the anterior part of the body, narrowing somewhat as it goes. It then widens out again rather suddenly to form a pear-shaped sac with rather stout muscular walls—the **stomach**. At the end of the stomach a distinct constriction—the **pylorus**—marks the commencement of the small intestine, the first portion of which, known as the **duodenum**, is bent sharply forwards so as to lie parallel to the stomach, to which it is attached by a membranous fold—the **gastro-duodenal omentum**. In this fold lies a small whitish-yellow elongated mass—the **pancreas**— which will be described farther on.

The small intestine bends sharply back again towards the posterior end of the animal, is thrown into several loops—its total length when straightened out being from four to five inches,—and then it passes suddenly into a much wider tube about an inch and a quarter long, the **large intestine**. The large intestine passes without any obvious line of demarcation into a short terminal portion, the **cloaca**, which opens to the exterior by the **anus**. A large thin-walled sac, **the urinary bladder**, opens into the ventral side of the cloaca, which receives other ducts connected with the kidneys and reproductive organs, to be described farther on.

In order to examine the œsophagus, stomach, and intestines, it has been necessary to turn aside a large lobulated reddish-brown organ which occupies the ventral region of the anterior half of the abdominal cavity. This is the **Liver**. It consists of three main lobes, a right, a left, and a median, united across the middle line by a comparatively narrow bridge of liver

tissue. The left lobe is much the largest, and is divided into two secondary lobes by a deep fissure extending forwards from its hinder margin. If the lobes of the liver be turned forwards, a round or oval vesicle, the **gall-bladder**, may be seen in the deep fissure between the right and left lobes. It has thin walls, and is generally full of a green fluid, the bile, which imparts its colour to the whole bladder. The gall-bladder receives bile from the liver by means of three ducts, which pass from the lobes of the liver, unite together, and enter the gall-bladder at its upper end as a single vessel, the **cystic duct.** The bile is carried from the liver and gall-bladder to the duodenum by a single duct, the **bile duct**, or **ductus choledochus,** which is formed by the union of three vessels arising from the cystic duct, and is joined, at some distance from its origin, by several vessels from the middle lobe of the liver.

The bile duct, in its passage towards the duodenum, traverses the whitish lobular gland which we have already noticed lying between the stomach and duodenum. This is the pancreas, a gland which secretes a solvent fluid, the pancreatic juice. The ducts of the pancreas join the bile duct about the middle of its course, and the common biliary and pancreatic duct opens into the duodenum on its dorsal surface about half-an-inch beyond the pylorus.

The liver and pancreas are the two glands which discharge their secretions into the alimentary canal by ducts. Both of them were formed, in the course of development, as outgrowths of the embryonic gut. The stomach and intestine are also glandular, their lining membrane being thrown into longitudinal folds for increase of surface; and the walls of these folds are studded with innumerable minute orifices, the openings of microscopically small gastric and intestinal glands, which discharge their secretions into the cavity of the gut. These glands are of very simple construction, being nothing more than finger-shaped depressions lined by the mucous membrane lining the gut. We shall study their characters more closely hereafter.

In studying the buccal cavity of the frog we noticed, on the floor of its hinder end, a slit-like aperture, the glottis. This opens into a short, wide tube, whose walls are strengthened by a rather complex set of cartilages. This tube is the **larynx.** The cartilages are five in number: a single curiously shaped

hoop, with various processes, called the **cricoid**; a pair of crescentic cartilages, placed in front of it, called the **arytenoids**; and a smaller pair, connected with these, called the **pre-arytenoids**. These cartilages are moved by special muscles, and they bear a pair of flat bands of connective tissue—the **true vocal cords**—lying parallel to one another, with a slit-like space between—the **rima glottidis**. The cartilages and muscles are so disposed that the edges of the vocal cords forming the sides of the rima glottidis may be approximated or separated, whilst the cords themselves are tightened or slackened The cords are thrown into vibration by the passage of air over their tightened and approximated edges, and thus a sound—the well-known croak of the frog—is produced. The male frog croaks much more loudly than the female, and its laryngeal cartilages are larger, thicker, and stronger. The croak of the male is further intensified by a pair of resonators, in the form of vocal sacs, which open one in each corner of the floor of the hinder part of the mouth. When the animal croaks the sacs are inflated, and bulge out under the angles of the mouth.

The **lungs** take their origin from the posterior part of the laryngeal tube, their openings being kept extended by a pair of curved cartilaginous processes of the cricoid. Each lung starts as a contracted tube from the larynx, and then swells out into a pear-shaped bag which lies in the body cavity dorsal to the liver. The lungs have highly elastic walls, which, by their contraction, expel the air in a dead frog and leave the lungs shrunken and collapsed. They are easily inflated by means of a blow-pipe inserted in the glottis. The internal structure of the lungs is somewhat complicated. The cavity of the sac, especially its upper part, is broken up into chambers by a number of folds or partitions passing into the interior. These chambers are further subdivided by secondary folds starting from their walls, and the smaller chambers so formed may again be subdivided in a similar manner into minute chambers termed **alveoli**. The whole of the upper part of the lung thus assumes a sort of honeycomb structure, but in its lower pointed end the chambers are less developed, and at the extreme apex are absent altogether, The honeycomb arrangement provides a large surface for exposure to the air contained in the lungs; and, as the partition walls are exceedingly thin, the blood which circulates through them is brought so close to the

air that an exchange of the gaseous constituents of blood and air is readily effected, the blood taking up oxygen and giving in return carbonic acid gas. The lungs, as appears from this description, are offsets of the alimentary tract, and they are formed, in the course of the growth of the tadpole into the frog, as an outgrowth from the ventral wall of the gut in the throat region, the outgrowth soon becoming bi-lobed to form the pair of lung sacs.

The other abdominal viscera of the frog are the spleen, the kidneys with the adrenal bodies, and the reproductive organs.

The **spleen** is a small, rounded-oval, dark-red body lying in the mesentery near the commencement of the large intestine. It belongs to the lymphatic system, and has no duct.

The **kidneys** are two elongated, flattened, dark-red bodies lying one on each side of the vertebral column towards the hinder end of the abdominal cavity. They lie in the large lymph space formed behind the peritoneal lining of this part of the cœlom, and, as they are covered over by the peritoneum, they are, like the gut and other organs which we have studied, outside the cœlom. Each kidney has a straight border turned towards the vertebral column, and a convex outer margin. The kidney consists of a number of convoluted tubules, the **uriniferous tubules**, bound together by fibrous connective tissue, and abundantly supplied with blood-vessels. The tubules open into collecting ducts, which unite together to form a single duct, the **ureter**, leading to the cloaca. The ureters are short, straight tubes which arise from the outer edges of the kidneys, and run backward, opening into the cloaca on its dorsal side, opposite the opening of the bladder. In the male frog each ureter presents a spindle-shaped dilatation on its outer side, the **vesicula seminalis**.

The **adrenal bodies** are found on the ventral sides of the kidneys, near their outer borders. They are small yellow patches, of somewhat doubtful function and significance.

The reproductive organs consist of the **testes** and their ducts in the male, the **ovaries** and their ducts in the female. The testes are a pair of ovoid pale-yellow bodies attached to the dorsal wall of the body cavity by a fold of the peritoneum, the **mesorchium**. They lie on the ventral sides of the kidneys, to which they are attached by a variable number of very fine

ducts, called the **vasa efferentia**. The sperm, which is formed in the testes, passes through the vasa efferentia into the collecting tubes of the kidney, and thence by the ureter to the vesicula seminalis and to the exterior. Thus in the male frog there is a common duct for both generative and urinary products, a fact of which we shall see the significance hereafter. The ovaries vary very much in size according to the season of the year. In the breeding season in early spring they are very large, and fill the body cavity to distention; in summer and autumn they are much smaller. They correspond in position with the testes—*i.e.* they are attached to the dorsal wall of the body cavity by a peritoneal fold, the **mesovarium**, and lie on the ventral sides of the kidneys. Each ovary is a large irregularly-lobed sac, which, when viewed externally, seems to be filled by a mass of spherical black and white bodies about the size of No. 5 shot. These are the **ova** or eggs. There are no ducts continuous with the ovaries; the ova, when ripe, escape by rupture of the ovarian walls, and fall into the body cavity, whence they are carried to the exterior by a pair of much coiled ducts, with funnel-like mouths opening into the body cavity. These are the **oviducts**. They lie external to the kidneys and ovaries, their mouths opening on either side into the anterior part of the body cavity not far from the middle line. Behind the mouth each oviduct has the form of a rather slender white tube, which gradually expands, maintains an even size throughout a much coiled course towards the posterior end of the body, and then widens out suddenly to form a pear-shaped dilation—the so-called uterus. The two uteri open close together into the cloaca just in front of the openings of the ureters. The walls of the coiled part of the oviducts are abundantly furnished with glands, which swell up during the breeding season and cause the oviducts to increase greatly in size. The peritoneal fold by which the oviducts are suspended is known as the **mesometrium**. (See fig. 6.)

The **cloaca**, into which the urinary and generative ducts open, is a short tube continuous with the rectum. From what precedes, it follows that it has, besides the opening of the bladder on the ventral side, one pair of orifices on the dorsal side in the male—viz. those of the common uro-genital duct;

and two pairs in the female—viz. those of the ureters and oviducts.

The **fat-bodies** should be noticed; they are finger-shaped fatty masses of a bright yellow colour lying in front of the testes or ovaries.

All parts of the frog's body are supplied with a nutrient fluid, the **blood**, by means of a system of blood-vessels which take their origin from a hollow muscular organ, the heart. In order that the relations of the blood-vessels to one another and to the heart may be clearly understood, it should be borne in mind that the blood is the great medium of exchange in the body. It brings nutrient material, collected from the walls of the alimentary canal, to the organs for their repair, and receives in exchange effete waste material which it carries away to organs—the kidneys and lungs—whose function it is to separate out the waste material and expel it from the body. A large part of this waste matter is carbonic acid gas, which is exhaled through the lungs; and the blood, in its passage through the lungs, receives in return oxygen which it carries to all parts of the body.

Bearing these facts in mind, we may study the mechanism by means of which the circulation of the blood is effected.

The heart is a hollow muscular organ, of roughly triangular shape, the apex pointing backward, lying in the mid-ventral line, immediately above the ventral ends of the shoulder-girdle and below the œsophagus. It is enclosed in a very thin membranous sac, the **pericardium**, on the ventral walls of which some muscular slips from the great internal oblique muscle of the abdominal wall are inserted. The pericardial cavity is a portion of the cœlom, which has been cut off from the remainder by the growth of a partition, in the substance of which run the great veins leading to the heart. Its relations are rather complicated, and will be better understood at a later stage; but it may here be noticed that the pericardial cavity is a ventral portion of the cœlom, cut off by the above-mentioned partition from a dorsal portion continuous behind with the abdominal cœlomic space, in which the lungs lie. The heart seems to lie in the pericardial cavity, but in reality it is outside of it, just as the gut and other abdominal viscera are seemingly inside, but really outside, of the abdominal portion of the cœlom. The pericardium has an extremely thin lining

membrane, which is reflected over the heart, and so excludes it from the cavity which it lines.

The heart itself consists of (1) two **auricles**, forming the wider anterior portion: they are readily distinguished by their thinner walls and darker colour, due to the blood being seen through their walls; (2) a single **ventricle**, situated posteriorly, with thick muscular walls, which are of a paler colour than those of the auricles; (3) the **sinus venosus**, a thin-walled sac, lying on the dorsal or hinder region of the heart, and formed by the union of three great veins; (4) the **truncus arteriosus**, a stout cylindrical vessel which arises from the ventral surface of the right-hand side of the base of the ventricle. Examining the structure of the heart more closely we find that the sinus venosus is a thin-walled sac of triangular shape, the apex of the triangle pointing backward. At its apex it receives a large blood-vessel, the **inferior vena cava**, and at each of its remaining angles, right and left, it receives a large vessel, the right and left **superior venæ cavæ**. The sinus venosus communicates by a transverse opening, guarded by two valves, with the right auricle. The valves at this opening are so disposed that they admit blood from the sinus venosus into the auricle, but prevent its passage in a reverse direction.

The two auricles together form a large thin-walled sac, of rather irregular but generally hemispherical shape, which opens below by an elongated slit into the ventricle. The sac is divided into two unequal parts by the auricular septum passing from the anterior wall to the auriculo-ventricular aperture, where it ends in a free concave border. Of the two auricles the left is decidedly the smaller, and in exceptional cases it is much smaller than the right. It receives at its upper dorsal surface, close to the auricular septum, a vein—the pulmonary vein—which brings blood back from the lungs.

The ventricle is much thicker than the auricles, through the presence of abundant muscular tissue in its walls. Its cavity is not smooth, but is rendered spongy in appearance, by the presence of numerous muscular ridges which project into it. The cavity does not extend far into the apex of the ventricle, is rather narrow dorso-ventrally, but elongated from right to left. The auriculo-ventricular aperture, by which the ventricle communicates with the auricles, is rather a wide opening, divided into two by the free edge of the auricular septum, and

guarded, on its ventricular side, by a pair of valves which have the form of flaps of membrane springing from the walls of the heart. One of these flaps is on the dorsal, the other on the ventral side of the aperture, and each is connected with the

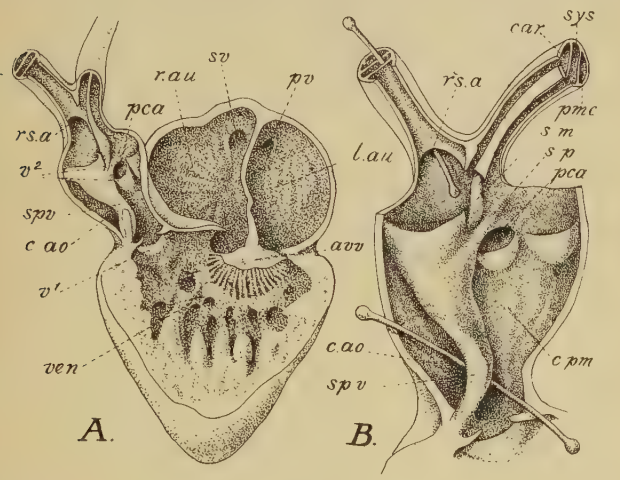

Fig. 7.

A, The frog's heart dissected from the ventral surface. *B*, an enlarged semi-diagrammatic view of the truncus arteriosus; the ventral wall has been cut through somewhat to the observer's right of the middle line, and the walls have been turned back. *avv*, auriculo-ventricular valve, with its cordæ tendineæ; *c.ao*, cavum aorticum of the truncus arteriosus; *car*, carotid artery; *c.pm*, cavum pulmonale of the truncus arteriosus; *l.au*, left auricle; *p.ca*, opening of the pulmo-cutaneous arches into the cavum pulmonale; *pmc*, pulmo-cutaneous artery; *pv*, opening of the pulmonary vein into the left auricle; *r.au*, right auricle; *r.sa*, opening of the right systemic artery; in *B* a rod is passed up the opening and projects from the cut end of the middle or systemic channel of the right aortic arch; *s.m*, septum medium of the upper part of the truncus; *s.p*, septum principale; *sp.v*, spiral valve, in *B* the reference line points to the surface of attachment to the ventral wall of the truncus which has been cut through; *sv*, opening of the sinus venosus into the right auricle; *sys*, systemic artery; v^1, proximal row of semi-lunar valves guarding the passage from the ventricle into the truncus; v^2, distal row of semi-lunar valves in the truncus; *ven*, ventricle.

muscular ridges of the ventricular wall by about a dozen very fine fibrous cords the **cordæ tendineæ**. The length of these cords is such that they allow the membranous flaps to rise up and meet one another in the middle line so as to close the aperture, but they prevent their rising farther into the cavity of the auricles.

The right-hand interior corner of the ventricle is prolonged on its ventral side, into a stout vessel, which passes forward and to the left across the auricles, and divides at the upper limits of the latter into two vessels, right and left, each of which almost immediately divides again into three. The large single vessel is called the **truncus arteriosus**. Though it appears single up to its bifurcation, the distal part of the truncus really consists of vessels closely united together, hence the truncus is conveniently subdivided into a proximal single portion, the **pylangium**, and a distal multiple portion, the **synangium**. The opening of the pylangium into the ventricle is large, and is guarded by three membranous valves, shaped like watch-pockets with their mouths turned towards the cavity of the pylangium. The free edges of each of these valves—known as the **semi-lunar valves**—are tied to the inner walls of the pylangium by cordæ tendineæ, similar to those of the auriculo-ventricular valve. Further, the cavity of the pylangium is incompletely divided into two by a membranous fold which commences on the ventral side close above the opening into the ventricle, runs forward with a spiral course, becoming deeper as its goes, and it ends on the dorsal and right side of the pylangium, where it is fused to one of the three semi-lunar valves, similar to those of the ventricular aperture, which guard the opening from the pylangium into the synangium. The ventral border of this fold hangs free in the cavity of the pylangium, and extends across two-thirds of its diameter when fully extended, dividing it into a chamber beginning on the ventral side and curving round to the right, the **cavum aorticum**, and another beginning on the dorsal side and curving round to the left, the **cavum pulmo-cutaneum**. The synangium is the wide but very short part of the truncus which lies in front of the three valves separating it from the pylangium. It is completely divided by a horizontal partition, called the **principal septum**, into a dorsal and a ventral chamber. The dorsal chamber communicates with the cavum pulmo-cutaneum by an aperture situated just above the middle and smallest of the three valves, and anteriorly it is continued into the pulmo-cutaneous arteries. The ventral chamber is divided by a vertical partition, called the **septum medium**, into two wide right and left passages. The left passage leads into the systemic aorta of that side. The right passage is

open behind to the cavum aorticum, and anteriorly it is continued into the carotid arteries and the right systemic aorta. We have already noticed that the truncus arteriosus bifurcates at its anterior end, and that each bifurcation very shortly divides into three vessels. The bifurcations themselves are triple in constitution, as may be seen by cutting them across, when each is observed to be made up of three vessels—an inner and ventral, the **carotid**; a median, the **systemic**; and a dorsal and outer, the **pulmo-cutaneous.** It is by means of these vessels that blood is conveyed from the heart to all parts of the body. Vessels which carry blood away from the heart are known as **arteries.** They have firm, elastic walls, which do not collapse when empty, and retain their circular section when cut across; their firmness is due to the relatively large amount of elastic tissue contained in their walls. **Veins** are vessels which carry blood back to the heart; they have softer and less elastic walls than arteries, and collapse when empty or when cut across. The arteries and veins are united in the tissues by exceedingly fine vessels, called **capillaries,** which can only be studied by the aid of the microscope.

The arterial system of the frog starts from the truncus arteriosus, and the three main branches on either side into which it divides. Of these three arches the carotids are the most anterior. Each runs round the œsophagus towards the dorsal surface, and, shortly after its origin, expands into a small almost spherical dilatation—the **carotid gland.** Just before it expands into the carotid gland the arch gives off a small branch, which runs inward and forward over the throat, nearly parallel to its fellow of the opposite side, giving off branches to the hyoid apparatus and the tongue. This is the **lingual artery.** The **carotid artery** arises from the outer border of the carotid gland, runs round the œsophagus towards its dorsal surface, and there turns forward to run beneath the base of the skull, where it divides into (1) the external carotid artery, whose branches supply the pharynx, palate, and orbit, and (2) the internal carotid, which passes through a foramen in the base of the skull and supplies the brain. Just before it turns forward to run under the base of the skull the carotid gives off a small backward branch which joins the systemic or second arch, and is known as the **ductus Botalli.** This duct,

though open in the very young frog, is usually closed in the adult and no longer admits the passage of blood. The second or **systemic** arch runs round the œsophagus on either side towards the dorsal surface, and then turns inward and backward to join its fellow in the middle line just below the vertebral column, at about the level of the sixth vertebra. The right arch is directly continuous with the **dorsal aorta**, which runs straight back beneath the vertebral column and the urostyle; the left arch opens into the dorsal aorta by a small opening, and is continued as the **cœliaco-mesenteric**

Fig. 8.

The Frog dissected from the right side to show the distribution of the chief arteries; semi-diagrammatic. *H*, heart; *tr*, truncus arteriosus; *ca'*, carotid arch; *l*, lingual artery; *ca*, carotid artery; *sy*, systemic arch; *œ*, œsophageal artery; *oc.v*, occipito-vertebral artery; *sc*, subclavian artery, cut short; *ao*, dorsal aorta; *cœl*, cœliaco-mesenteric artery, supplying the viscera; its three main branches are indicated but all its subdivisions cannot be shown; *ra*, uro-genital arteries; *Il*, iliac arteries; *Pc*, pulmo-cutaneous arch, dividing into *p*, the pulmonary artery supplying the lung, and *cu*, the cutaneous artery, cut short; *La*, larynx; *S*, stomach; *I*, intestine; *R*, rectum; *Bl*, bladder; *M*, muscular abdominal wall turned back; *K*, kidney.

artery, passing to the stomach and intestines. The systemic arches give off on either side before they unite to form the dorsal aorta (1) a **laryngeal** artery, a small vessel arising from the proximal part of the arch, and passing forward to supply the larynx; (2) an **œsophageal artery**, arising from the dorsal side of the upper part of the arch, and turning downward to supply the œsophagus; (3) an **occipito-vertebral artery**,

arising from the dorsal side of the arch opposite the transverse process of the second vertebra, and dividing after a short course into two branches (*a*) the **occipital artery**, which courses forward, supplying the sides of the head and the jaws, (*b*) the **vertebral artery**, running backward parallel to the vertebral column, and dorsal to its transverse processes: it gives off branches to the muscles of the body and to the spinal cord; (4) a **subclavian artery**, arising from the arch close behind the occipito-vertebral, and supplying the shoulder and fore-limb.

The cœliaco-mesenteric artery, which arises from the left arch just at its point of union with its fellow, soon divides into two branches, the **cœliac** and the **mesenteric**. The cœliac artery is further divided into the **gastric artery** supplying the stomach, and the **hepatic**, supplying the liver. The mesenteric artery divides into an anterior and a posterior branch and into the **splenic artery**, which goes to the spleen. In its further course backward the dorsal aorta gives off from four to six small vessels from its ventral side, to supply the kidneys and generative organs, and some small vessels from its dorsal side, which supply the muscles of the back and sides. These are the **uro-genital** and **lumbar arteries**. Opposite the middle of the urostyle the dorsal aorta bifurcates to form the **iliac arteries** which are continued onward as the **sciatic arteries** into the hind limbs.

The third or **pulmo-cutaneous** arches divide, after a short course on either side of the œsophagus, into the **pulmonary artery**, which supplies the lungs, and the **cutaneous artery**, a large vessel running up to pass close behind the ear, and then turning sharply backward to be distributed over the skin of the trunk.

The principal arteries which have been detailed above divide and subdivide in the various regions of the body to which they are distributed; the walls of their branches become thinner and less elastic, till finally they end in networks of extremely fine vessels with very thin walls, called capillaries. The capillaries may easily be studied, by the aid of the microscope, in the web of the frog's foot when the toes are stretched apart. They present the form of a network of fine tubes running through the tissues of the web. The meshwork is irregular, but, speaking generally, the capillaries

form numerous loops of various sizes, and the capillary tubes themselves unite freely with one another. Their walls are so thin that they are hardly apparent, but the blood stream coursing through their cavities is readily recognisable. The capillary tubes vary in diameter from $\frac{1}{2000}$th to $\frac{1}{1500}$th of an inch.

The capillaries are continuous, on the one hand, with the ultimate subdivisions of the arteries. On the other hand, they unite to form larger, but still very small vessels, the ultimate subdivisions of the veins, also called **venules**. Both arterioles and venules are distinguished from capillaries by their walls, which are thickened by the presence of muscular fibres and connective tissue. The elastic layer, which is a conspicuous element in the walls of larger arteries, dies out in the smallest arterioles.

The venules unite together and are gathered into larger and larger vessels, the **veins**. Veins are vessels which convey blood back to the heart. Their walls have much the same structure as those of arteries, but there is much less elastic tissue and much more connective tissue in them; hence they are less resilient, but at the same time tougher than arteries. We may consider the veins under three heads: (1) those bringing blood back to the heart from the head, throat, and fore-limbs; (2) those bringing back blood from the viscera, the trunk, and hind limbs; and (3) those bringing back blood from the lungs.

Blood is brought back from the tongue and from the lower jaw by two veins, known as the **lingual** and **mandibular** veins (*l* and *m* fig. 9). These unite on the ventral wall of the throat to form a single vessel, the **external jugular** vein, which, after a short course, is joined by an **internal jugular** vein bringing blood back from the inside of the skull. It leaves the skull by an aperture at the hinder border of the orbit. Just before it unites with the external jugular the internal jugular receives a small **subscapular** vein bringing back blood from the shoulder and back of the fore-limb. The short section lying between the union of the subscapular with the internal jugular and the external jugular is generally distinguished as the **innominate** vein. The single vessel formed by the union of the external jugular and innominate is almost immediately joined by a third large vein, the **subclavian**. The

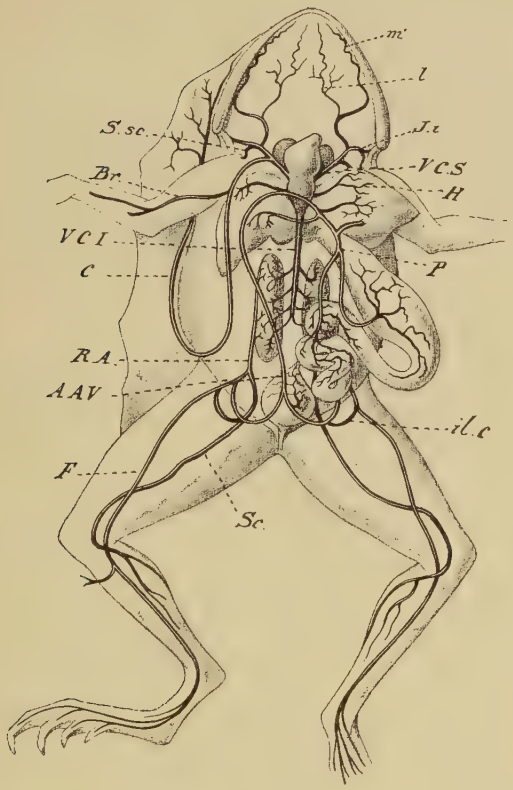

Fig. 9.

Diagram of the venous system of the Frog. The apex of the heart is turned forward to show the sinus venosus. *m*, mandibular vein; *l*, lingual vein; *Ji*, internal jugular vein; *S.sc*, subscapular vein; *Br*, brachial vein; *C*, musculo-cutaneous vein; *VCS*, vena cava superior; *VCI*, inferior vena cava; *H*, hepatic veins; *F*, femoral vein; *Sc*, sciatic vein; *RA*, renal portal vein; *ilc*, ramus communicans iliacus; *AAV*, anterior abdominal vein, formed by the union of two pelvic veins; *P*, portal vein. The pulmonary circulation is not represented in the figure.

subclavian vein, which, as its name implies, lies under the clavicle and precoracoid, is itself formed by the union of two veins—the **brachial** which brings blood from the fore-limb, and the **musculo-cutaneous**, a very large vein which takes its origin in the nose, runs straight backward as far as the middle of the trunk, receiving branches from the skin and muscles of the side of the body, and then turns sharply forward to pass up the ventro-lateral wall of the body and join the brachial. The three veins, external jugular, innominate, and subclavian, unite to form the **superior vena cava** of their side of the body, a wide vessel which runs into an anterior angle of the sinus venosus. The systems of the right and left venæ cavæ anteriores are similar, and the above description serves for either side of the body.

There are, then, two anterior venæ cavæ opening into the two anterior angles of the triangular sinus venosus. But there is only one **posterior vena cava** opening into the posterior angle of the sinus venosus and bringing back blood from the abdominal viscera, the trunk, and hind limbs. The system of the posterior vena cava is complicated. It arises between the kidneys, where it is formed by the union of four or five **renal** veins from each side, and by the **ovarian** or **testicular** veins in the female or male. It passes straight forward in the median line, is partly enveloped by the substance of the liver, and, just before it enters the sinus venosus, it receives the **right and left hepatic** veins from the liver. The blood from the hind limbs, and from the other abdominal viscera, reaches the vena cava only after an indirect course through either the liver or kidneys.

The blood from the hind limb is returned to the pelvic region by two veins—the **femoral**, which twists round from back to front of the thigh to reach the ischial region of the pelvis, and the **sciatic**, which comes up from the back of the thigh to pass under the iliac bone of its side. The sciatic vein is almost directly continuous with a vein known as the **renal portal vein**, which passes forward to the outer border of the kidney, and there breaks up into small vessels which open into the capillaries of the kidney. The femoral vein divides at the root of the thigh into two branches. The dorsal branch, known as the **iliac vein**, runs forward in the dorsal side of the posterior part of the abdominal cavity, and unites with the

sciatic vein to form the **renal-portal.** The femoral and sciatic veins are further connected by a small vessel, the **ramus communicans iliacus**, which runs transversely from one to the other at the base of the thigh. The second or ventral branch of the femoral vein is known as the **pelvic vein**; it passes inward towards the mid-ventral line of the abdominal wall, and unites, just in front of the pubic cartilages, with its fellow of the opposite side to form the **anterior abdominal vein.** This is a large, median, unpaired vessel, which receives at its point of origin the **vesical vein** from the bladder, and then courses forward in the middle line of the ventral wall of the abdomen till it reaches the xiphoid cartilage of the sternum. It then turns inward and divides into three branches, two lateral and one median. The two lateral branches pass to the right and left lobes of the liver respectively, and break up in its substance into capillaries; the median branch unites with the **hepatic portal vein.**

The last-named vessel brings blood from the stomach and intestines. It is formed by the union of the **intestinal, gastric** and **splenic** veins, runs forward in the mesentery, and passes into the left lobe of the liver, where it breaks up into capillaries. Just before it enters the liver the hepatic portal vein is joined by the descending branch of the anterior abdominal. The blood from the liver is collected by the right and left **hepatic** veins, which open into the inferior vena cava just before it passes into the sinus venosus. We have seen that the lungs are supplied with blood by the two pulmonary arteries, each of which courses down to the outer surface of the lung sac to which it belongs from base to apex, giving off a number of branches as it goes. The blood, after passing through the lung capillaries, is gathered by venules, which unite to form the venous vessel lying along the inner side of the base of each lung. These right and left pulmonary veins run above the corresponding venæ cavæ, and unite to form a single trunk, the **common pulmonary vein,** which opens into the left auricle. We are now in a position to review the course of the circulation of the blood in the frog. The blood from the head and fore limbs, as well as that brought back by the musculo-cutaneous veins, passes straight into the sinus venosus by way of the superior venæ cavæ. But the blood coming from the hind limbs and from the posterior part of

the trunk and the abdominal viscera takes a much more complicated course.

The blood brought from the hind limbs by the femoral vein may take one of two paths. It may either go by way of the iliac veins to join the blood brought by the sciatic veins, and pass on by the renal-portal veins to the kidneys; or it may go by way of the pelvic and anterior abdominal veins to the liver. In either case it has, whether in the substance of the kidney or in the substance of the liver, to pass a second time through a system of capillaries, and to mingle with the blood brought to those organs by the renal and hepatic arteries respectively. Similarly, the blood returned from the stomach and intestines has to pass a second time through capillaries in the liver. Eventually, the blood from the capillaries of the kidneys and liver finds its way by the inferior vena cava into the sinus venosus. When veins do not pass direct to the heart from the organs and tissues in which they originate, but go to some other organ and sub-divide in it to join its capillary system, they are called **portal veins**, and the whole system of double capillary circulation is called a portal system. Thus in the frog we have a **renal-portal** and a **hepatic-portal** system, and renal-portal and hepatic-portal veins. These portal systems are very characteristic of the great group of Vertebrate animals, but a renal-portal system is only found in its lower members. The higher Vertebrata have only a hepatic-portal system.

The walls of the sinus venosus are feebly muscular and contractile. The beat of the frog's heart starts in the sinus venosus, which, by its contraction, forces blood through the sinu-auricular aperture into the right auricle, whence its return is prevented by the valves by which that aperture is guarded. At the same time the left auricle is filled with blood returned from the lungs by the pulmonary veins. The blood brought into the sinus by the venæ cavæ, and passed thence into the right auricle has passed through the capillaries of the body, where it has been robbed of a considerable portion of its oxygen, and has received a quantity of carbonic acid. In consequence of its poverty in oxygen it has a dark purplish hue, and is known as venous blood. But that coming from the lungs has parted with its excess of carbonic acid, and has

taken up oxygen from the air contained in the lungs; it is of a bright scarlet colour, and is known as arterial blood.

The muscular contraction which started in the sinus venosus spreads over the auricles, which contract simultaneously, and drive the blood onward through the wide auriculo-ventricular aperture into the single ventricle. The return of blood from ventricle to auricles is prevented by the membranous valve described above. As the right auricle contains venous and the left auricle arterial blood, the transversely-elongated cavity of the ventricle is filled with both kinds, the venous blood being on the right side nearest the opening of the truncus arteriosus, the arterial blood farthest away from it on the left. In the middle of the ventricular cavity the blood is, of course, mixed. The contraction of the ventricle follows immediately upon that of the auricles. The auriculo-ventricular valves close, and the blood is forced into the truncus arteriosus, the venus blood on the right side passing first. The wave of contraction passes forwards over the truncus from the base of the ventricle to the roots of the aortic arches, and any reflux of blood into the ventricle is prevented by the closing of the semi-lunar valves which guard the two ends of the pylangium.

On entering the pylangium the blood is necessarily directed by the spiral valve. It therefore passes from the dorsal side round to the right and thence to the ventral side of the truncus, and the venous blood passing over the free border of the upper end of the spiral valve enters the cavum pulmo cutaneum. Now, the arteries are already distended with blood under considerable pressure, which was only prevented from returning into the truncus by the semi-lunar valves at the distal end of the pylangium. This pressure is overcome by the blood forced forward at greater pressure by the contractions of the ventricle and pylangium, and the semi-lunar valves are forced open. In the synangium the blood newly arrived follows the path of least resistance, which is found in the wide aperture of the pulmonary artery. The first gush of nearly entirely venous blood therefore passes to the lungs, but as it fills the vessels of the lungs the resistance in them becomes as great as or greater than that in the synangium and other aortic arches. The next succeeding portion of the blood, which is now mixed arterial and venous

from the middle of the ventricular cavity, finds the least resistance in the wide openings of the right and left systemic arches, which are accordingly filled with mixed blood until their resistance becomes as great as, and greater than, that of the carotid arches, the resistance in which has been considerable, both because of their small diameter and because the flow of blood through the carotid arteries is impeded by the carotid glands. Thus the last portion of the blood, consisting of nearly pure arterial blood from the left end of the ventricular cavity, passes into the carotids.

We have seen how the arterial blood in the carotids is distributed to the head, there to pass into the capillaries of the tissues, to part with its oxygen, take up carbonic acid, and eventually to return by the superior vena cava to the sinus venosus. Similarly, the mixed blood in the systemic arches is distributed to the trunk, viscera, and hind-limbs by the dorsal aorta and its branches, and is collected and returned by the veins in the manner already described. The venous blood which enters the pulmonary artery goes to the lungs, takes up oxygen, parts with its excess of carbonic acid, and is returned to the left auricle by the pulmonary veins.

The frog, therefore, has a greater and a lesser (pulmonary) circulation, the blood in the former case making its circuit through the tissues of the body, in the latter through the shorter circuit of the lungs. The two circuits, however, are not closed off from one another, as they are in the higher vertebrates, but have a common starting-place in the single ventricle of the heart.

There remains but one set of organs and tissues for us to consider, the nervous system and the organs of special sense associated with it.

The nervous system consists of the **cerebro-spinal axis** and its nervous branches, and the **sympathetic ganglion chain.** The cerebro-spinal axis lies, as we have already seen, in the cranium and in the canal formed by the neural arches of the vertebral column. That part which lies in the cranium is the **brain**; and that part which lies in the neural canal of the vertebral column is the **spinal cord**.

The spinal cord is a cord of nervous tissue extending from the foramen magnum into the urostyle. It is not circular in section, but somewhat flattened dorso-ventrally, and is traversed

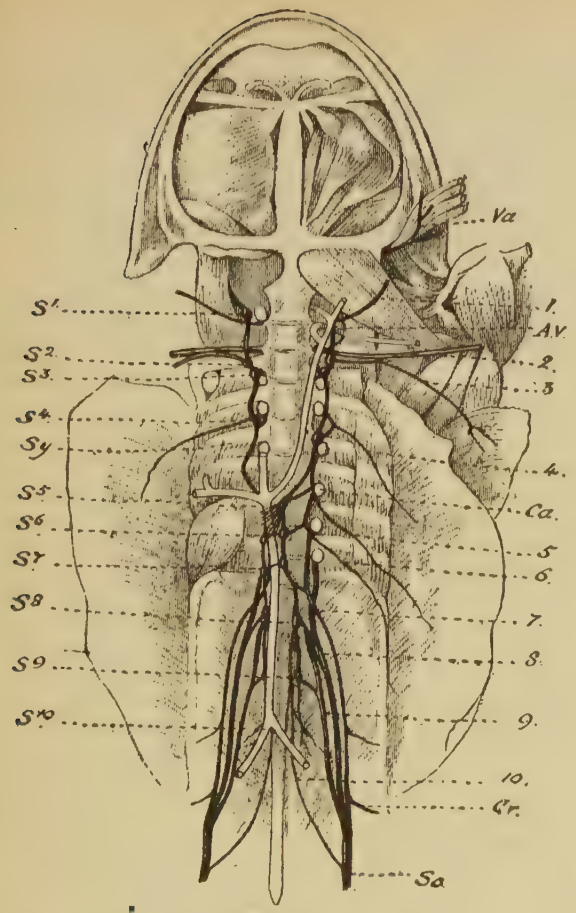

Fig. 10.

A dissection of the Frog from the ventral surface to show the origins of the spinal nerves and their connection with the sympathetic system. The nerves are drawn black; the dorsal aorta and its branches are left white. *1*, the first spinal or hypoglossal nerve; *2*, the second spinal or brachial nerve joined by *3*, the third spinal nerve; *4*, *5*, *6*, successive spinal nerves; *7*, *8*, *9*, three large spinal nerves uniting to form *Sc*, the great sciatic nerve, which also receives a branch from *10*, the tenth spinal nerve; *Sy*, the main sympathetic trunk; *S1*—*S8*, successive sympathetic ganglia united to the spinal nerves by communicating branches of varying length; *AV*, annulus of Vieussens (the loop has been drawn too large); *Ca*, calcareous bodies near the exits of the spinal nerves; *Cr*, the crural nerve.

both dorsally and ventrally by a median longitudinal narrow cleft or fissure—the dorsal and ventral fissures,—but neither of these extends to its most posterior part. Nor is the cord of the same diameter throughout, but it is swollen in the regions of the second and third, and again in the regions of the fifth and sixth vertebrae to form the brachial and sacral enlargements. Posteriorly to the seventh vertebra the cord thins out rapidly, and is continued into the urostyle as a slender thread, the **filum terminale**.

Ten pairs of nerves are given off from the spinal cord to the trunk and limbs. The first of these, which marks the commencement of the spinal cord (for there is no other demarcation between it and the hindmost part of the brain), passes out by the inter-vertebral foramen between the first and second vertebrae. It courses round the side of the throat, coming near to the surface just behind the angle of the lower jaw, and there it turns forward and runs to the root of the tongue. This nerve is known as the **hypoglossal**. The second spinal nerve is large; it leaves the neural canal in the foramen between the second and third vertebrae, and passes straight outward, supplying branches to the shoulder-girdle and arm; hence it is called the **brachial** nerve. It is joined more or less completely, at a little distance from its exit from the vertebral column, by the third spinal nerve. The two nerves supply a number of small branches beyond the point where they unite; and these branches, inosculating with one another, form a network known as the **brachial plexus**. The fourth, fifth, and sixth spinal nerves run obliquely backward from the inter-vertebral foramina proper to them, and supply the muscles of the trunk. The seventh, eighth, ninth, and tenth spinal nerves (the last-named passing out of the foramen of the urostyle) run obliquely backward to the region of the pubis, and there the seventh and eighth unite to form a single trunk, which is joined a little farther back by the ninth, and, a little farther back still, by a branch of the tenth. The large nerve so formed is the **sciatic**, and the network formed by the union of the nerves which are combined in it is called the **sciatic plexus**.* As the spinal cord narrows rather suddenly in the region of the sixth nerve, the roots of the seventh, eighth,

* The details of the sciatic plexus are subject to some variation, but the arrangement described here may be considered normal.

ninth, and tenth start from the spinal cord considerably in front of the inter-vertebral foramina through which they successively pass to the exterior, and they form, together with the filum terminale, a bunch of parallel cords lying inside the posterior part of the neural canal, and called the **cauda equina.** The **crural nerve** arises from the seventh spinal at or just before its union with the eighth, and runs to the ventral and outer border of the thigh, supplying the muscles and skin of that region.

The **sciatic nerve** is the largest in the frog's body, and is of great importance in certain physiological experiments. It passes into the leg close to the posterior end of the urostyle, and runs down between the muscles of the thigh on the inner or hinder side, following, in its course, the biceps muscle of the thigh. In the upper part of its course it gives off several branches to the thigh muscles, and a little way above the knee it divides into two branches, the **peroneal** and the **tibial** nerves. The former runs down the crus on the outer side of the tibio-fibula, and is eventually distributed to the foot. The tibial nerve runs down the crus on the inner border of the gastrocnemius muscle, giving off branches to it, and eventually supplies the sole of the foot.

The tenth spinal nerve, which passes through the small coccygeal foramen in the urostyle, besides contributing a branch to the sciatic, sends twigs to the bladder, the cloaca, and the adjacent parts.

Each of the spinal nerves arises from the spinal cord by two roots, a dorsal or posterior, and a ventral or anterior root. The dorsal root is also called **sensory** or **afferent,** because it is composed of fibres, which only transmit impulses from without inwards—from the tissues to the spinal cord and brain. The ventral roots are also known as **motor** or **efferent,** because their fibres only transmit impulses in the reverse direction, from the cerebro-spinal axis to the tissues. The two roots unite to form one just as they pass out through the inter-vertebral foramina, and the dorsal afferent root has an enlargement or ganglion on it just before it joins the ventral root. The spinal nerves are connected with the sympathetic nervous system, but before describing this it will be well to consider the brain and cranial nerves.

The brain is directly continuous with the spinal cord, and

a small canal, which traverses the centre of the latter, expands into the brain to form a series of chambers known as the **ventricles** of the brain.

The brain may he considered as consisting of three parts—the hind-brain, the mid-brain, and the fore-brain.

The hind-brain of the frog is a somewhat enlarged but direct forward continuation of the spinal cord. It has two divisions, the **medulla oblongata** (also called the **bulb**, or **myelencephalon**) and the cerebellum (**metencephalon**). The spinal cord, as it passes forward into the bulb, widens out, its floor becomes thicker, its roof very much thinner, and its central canal widens out to form a triangular cavity, the **fourth ventricle**, whose exceedingly thin roof is covered over by a very vascular membrane. The cerebellum, relatively large in many vertebrates, is represented in the frog by a narrow band of nervous tissue lying tranversely over the most anterior part of the bulb. The mid-brain (**mesencephalon**) lies immediately in front of the hind-brain and in a line with it. Its roof is formed by a pair of ovoid swellings, called the **optic lobes** or **corpora bigemina**; its floor, which is thick, consists chiefly of nerve fibres running forward from the bulb to the fore-brain. Each optic lobe is hollow, and its cavity communicates with a narrow passage called the **Sylvian aqueduct**, leading from the cavity of the fourth ventricle to the cavity of the fore-brain in front. This passage is sometimes called the "**iter**." *Iter a tertio ad quartum ventriculum.*

The fore-brain consists of two parts, the **thalamencephalon** behind, and the **cerebral hemispheres** or **prosencephalon** in front. The side walls of the thalamencephalon are thickened to form the **optic thalami**, but its roof and floor are thin, and the former is covered over by a very vascular membrane, just as is the roof of the fourth ventricle. By reason of the thickening of its lateral walls, and the thinning out of its floor and roof, the cavity of the thalamencephalon, known as the **third ventricle**, is deep dorso-ventrally but narrow from side to side. Its floor is produced into a conical depression, the **infundibulum**, and its roof is produced into a hollow finger-like projection, on the top of which is borne a rounded vascular body usually known as the **pineal gland**. It appears, however, that what is usually called the pineal gland is nothing more than a thickened portion of the choroid plexus or

vascular membrane which covers this part of the head. The true pineal gland is a small vesicle lying outside the skull beneath the skin. In the embryo this vesicle is connected by a pedicle with the roof of the thalamencephalon, but in the adult frog the connection is lost, and there is no foramen between the parietal bones whereby the pineal gland can make communication with the brain. All that remains inside the skull, therefore, is the hollow pedicle. The pineal body is a structure of much interest which occurs in the brains of all Craniata. The older anatomists fancifully described it as being the seat of the soul, but it really is the relic of a once well-developed and functional sense-organ, having the character of an eye, with lens, retina and nerve, the last being represented by the pedicle. Such an eye, in a more or less degenerate condition, actually occurs in several living reptiles, and in them there is a distinct foramen between the parietal bones through which the nerve or pedicle passes to the eye. This parietal foramen is obsolete in living Batrachia, but was universally present in certain extinct Amphibia—the **Stegocephalia**,—and it is inferred that in them the pineal eye was well developed and functional. It is worthy of remark that the pineal organ, though it has the structure of an eye, does not resemble the paired eyes of Vertebrata, but rather resembles those of certain Invertebrata.

In front the third ventricle is bounded by a wall of nervous tissue called the **lamina terminalis**. Right and left of this a passage leads into the cavities of the foremost division of the fore-brain, the **cerebral hemispheres**, which together constitute the **prosencephalon**. The hemispheres are ovoid bodies of considerable size relatively to the other parts of the brain. Their smaller ends are directed forward, and produced in front into two rounded swellings, the **olfactory lobes**, or **rhinencephala**. The hemispheres are united together before and behind by the fusion of their inner walls, but are completely separated from one another in their middle portions by a deep vertical cleft extending from the dorsal to the ventral surface. The rhinencephala are fused together by their inner walls, but both in them and in the fused portions of the cerebral hemispheres, shallow median furrows on the dorsal and ventral surfaces mark their double origin.

The cavities of the cerebral hemispheres are known as the

lateral ventricles. They are separate from one another, but

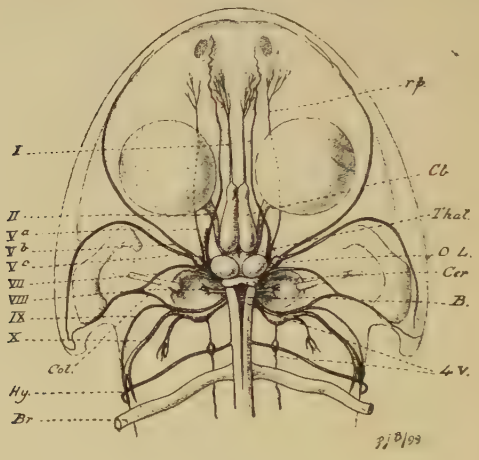

Fig. 11.

The Brain, Cranial Nerves, and anterior part of the Spinal Cord of the Frog dissected from the dorsal surface. *Cb*, cerebral hemispheres; *Thal*, Thalamencephalon; in the middle of it is seen the hole by which the stalk of the pineal body communicated with the cavity of the third ventricle; *O L*, corpora bigemina (mid-brain); *Cer*, cerebellum; *B*, the bulb or medulla oblongata; *4V*, the fourth ventricle; *I*, the olfactory or first pair of cranial nerves; *II*, the optic, second pair of cranial nerves; *Va*, the ophthalmic branch of the trigeminal or fifth pair of cranial nerves; *Vb*, the maxillary branch, and *Vc*, the mandibular branch of the trigeminal. The two last branches spring from a large swelling on the main stem of the nerve; this is the Gasserian ganglion; *VII*, the main branch of the facial or seventh pair of cranial nerves crossing over *Col*, the columella auris, and just beyond this sending back a branch to connect with the ninth nerve; *rp*, the ramus palatinus of the seventh nerve, passing below the eyeball and distributed to the skin on the snout and anterior part of the palate; *VIII*, the auditory or eighth pair of cranial nerves; *IX*, the glossopharyngeal or ninth pair of cranial nerves; *X*, the pneumogastric, vagus, or tenth pair of cranial nerves. The vagus has a large ganglion on its root which is joined by the anterior extension of the sympathetic system coming from the first sympathetic ganglion lying under *Hy*, the hypoglossal or first pair of spinal nerves; *Br*, the brachial second pair of spinal nerves. The third, fourth, and sixth pair of cranial nerves passing to the muscles of the eyeball are not shown in the figure.

each opens by a short narrow passage into the third ventricle

just behind the lamina terminalis. The Y-shaped opening thus produced is known as the **foramen of Munro**. The lateral ventricles are ovoid cavities with rather thin walls in the embryo, but, as growth proceeds, the anterior and inner part of the wall of each becomes much thickened, and bulges into the cavity, reducing it to a crescentic slit in its lower portion. The thickened prominences are known as the **corpora striata.**

Ten pairs of cranial nerves are given off from the brain.

The first pair springs from the anterior end of the rhinencephala, and passes straight to the olfactory chambers; these are the **olfactory nerves**. The second or **optic** pair arises from the sides of the brain beneath the optic lobes. Each nerve starts as a broad band of fibres which runs forward and downward to meet its fellow of the opposite side on the under surface of the thalamencephalon just in front of the infundibulum. Here most if not all of the fibres of the optic nerves cross over to the opposite side, the point of their decussation being called the **optic chiasma**. From the chiasma each nerve runs outwards through a foramen in the cranial wall, and passes into the eyeball.

The third, fourth, and sixth pairs of cranial nerves are distributed to the muscles of the eye.

The eyeball is moved by six muscles passing from its equator to the walls of the orbit. Four of these, attached close together to the inner posterior angle of the orbit, are known as the **recti muscles**, and are attached respectively to the upper (**rectus superior**), lower (**rectus inferior**), posterior (**rectus posterior**), and anterior (**rectus anterior**) sides of the eyeball. In addition to these a muscle arising from the anterior inner angle of the orbit passes obliquely backward, and is inserted on the lower surface of the eyeball (**inferior oblique**), and another (the **superior oblique**), arising close to the origin of the inferior oblique, passes obliquely upward and backward and is inserted on the upper surface of the eyeball. These muscles occur in all craniate vertebrates; the frog has in addition a **musculus retractor bulbi**, which partly surrounds the optic nerve, and lies within the cone formed by the four recti muscles. The third nerve, called the **motor oculi,** supplies the recti superior, inferior, and anterior, and the obliquus inferior. The fourth nerve supplies the superior oblique, and is known as the **pathetic** or **trochlear** nerve. The

sixth, or **abducens** nerve, passes to the posterior rectus and gives off a branch to the retractor bulbi. The third nerve rises from the floor of the mid-brain near the median line, the sixth pair from the ventral surface of the medulla, and also close to the median line ; but the fourth pair differs from all the other cranial nerves in arising from the dorsal side of the brain between the medulla and optic lobes.

The fifth pair of nerves, called the **trigeminal**, is the largest of the cranial nerves of the frog. The nerve of each side arises from the side of the anterior end of the medulla oblongata, runs outward and forward to the cranial wall, and passes through a foramen which is partly bounded by a notch in the inner side of the pro-otic bone. Just before it reaches the foramen the trigeminal swells out to form the large **Gasserian ganglion**. After passing through the foramen the nerve runs along the anterior face of the auditory capsule and divides at once into two large branches, the **ophthalmic branch** and the **maxillo-mandibular branch**. The ophthalmic branch runs forward close to the cranial wall between it and the eyeball. At the front end of the orbit it divides into two nerves which pass through apertures in the walls of the olfactory capsule and supply the nose and the skin of the front of the head. The maxillo-mandibular nerve, after a short course in front of the auditory capsule, divides into two branches—an upper, the **maxillary nerve**, which runs forward and outward between the eyeball and the lower and outer wall of the orbit to the margin of the upper jaw, and the lower **mandibular nerve**, which turns backward, outward, and downward to the squamosal bone, and passes across to the lower jaw, where it runs forward on the outer side to the symphysis.

The seventh, or **facial nerve**, arises from the medulla, close behind the fifth, and runs forward close to the Gasserian ganglion, with which it unites. It leaves the cranium in close company with the mandibular branch of the trigeminal, and divides at once into (1) a **palatine branch**, which runs forward on the floor of the inner side of the orbit, and eventually makes connections with the maxillary branch of the fifth, and supplies the roof of the mouth ; (2) a **hyomandibular branch**, which runs outward and backward across the wall of the auditory capsule to reach the columella auris ; crossing over

the inner end of this, it turns down to the eustachian tube and angle of the mouth. The seventh is joined close to the columella by a branch from the ninth.

The eighth, or **auditory nerve**, arises from the medulla, immediately behind the seventh, goes straight through a foramen in the auditory capsule to the ear, and supplies the organ of hearing.

The ninth, or **glossopharyngeal nerve**, arises, in common with the tenth nerve, from a number of roots on the side of the medulla, behind the auditory nerve. It passes, in company with the tenth nerve, through a foramen at the back of the cranium just in front of the occipital condyle, and divides into two branches, an **anterior**, which runs forward to join the facial nerve close to the columella, and a **posterior**, which curves downward and inward to the floor of the pharynx, along which it runs, supplying the petrohyoid muscles and the mucous membrane of the tongue and pharynx.

The tenth, **pneumogastric** or **vagus** nerve, is a very important nerve with complicated relations. After leaving the skull in company with the ninth nerve, it enlarges to form a ganglion, the **ganglion nervi vagi**. The nerve runs backward and ventralward along the side wall of the pharynx, and finally divides into several branches, of which the most important are: (1) the **nervus recurrens** or **laryngeus**, which arrives at the posterior cornu of the hyoid, and turns forward to pass beneath it and the pulmo-cutaneous artery, whence it runs forward close to the middle line, to end in the larynx; (2) the **ramus cardiacus**, which runs along the dorsal surface of the pulmonary artery and the superior vena cava towards the sinus venosus, where it joins its fellow of the opposite side, and the two pass on to the auricular septum of the heart; (3) the **rami gastrici**, which run through the partial diaphragm formed by the insertion of the internal oblique muscle upon the walls of the œsophagus, and are distributed to the walls of the stomach; (4) the **rami pulmonales**, which also perforate the partial diaphragm, and then follow the course of the pulmonary artery to the lung.

The sympathetic nervous system (see fig. 10) is intimately connected with both spinal and cranial nerves. It is a chain of paired nervous ganglia, joined together by longitudinal cords, lying on either side of the vertebral column, and each ganglion makes connection with a spinal nerve by a short branch, the

ramus communicans. In the anterior part of the body the sympathetic chains lie right and left of and parallel to the vertebral column ; at about the level of the sixth vertebra they approach one another in the middle line, and become closely connected with the dorsal aorta, alongside of which they run. The first sympathetic ganglion lies on the hypoglossal nerve, close to its exit from the first inter-vertebral foramen. Its ramus communicans is represented by a few fine and very short fibres connecting the ganglion with the nerve. From the ganglion two or three nervous strands pass backward, one passing beneath and one or two above the brachial artery, so as to encircle it, as it were, with a ring. This ring is known as the **annulus of Vieussens**. The second ganglion lies on the brachial nerve ; it is the largest of the whole series, and, like the first, is connected with the spinal nerve by a few fine fibres which do not form a distinct ramus communicans. The third ganglion is usually fused with the second, but has a short and distinct ramus communicans with the third spinal nerve. After this point the sympathetic chain follows the course of the systemic aortic arch, and when this joins its fellow to form the dorsal aorta the sympathetic chains follows the course of the latter. Being thus farther removed from the vertebral column, the rami communicantes become longer. There are as many sympathetic ganglia as there are spinal nerves, and each makes communication by its ramus communicans with the spinal nerve proper to it. Thus the fourth, fifth, sixth, and successive spinal nerves up to the tenth, supply each a ramus communicans to a sympathetic ganglion, the tenth nerve being peculiar in making several connections—as many as ten or twelve in some cases—with the sympathetic chain, but the number is not constant. The seventh, eighth, and ninth are also said to have two or three communications apiece with the sympathetic chain.

The sympathetic chains of each side are connected by numerous fine twigs, which surround the dorsal aorta and form a plexus around it, and from this plexus very fine nerves pass to the adjoining organs. The sympathetic system is characterised by the fact that its branches divide and subdivide, and the sub-divisions interlace and anastomose with one another to form networks or plexus which include numerous ganglia. The two most important of these are :

(1) the **cardiac plexus**, formed by nerves arising from the first ganglion of the chain. It lies on the auricles and surrounds the great blood-vessels at their openings into the heart; (2) the **solar plexus**, formed by branches from the third, fourth, and fifth ganglia, and lying on the dorsal side of the stomach. Anteriorly the sympathetic chain makes communications with the cranial nerves by a branch which passes on either side from the first ganglion to the ganglion nervi vagi, where some of its fibres enter the vagus, the remainder pursuing their forward course to enter the Gasserian ganglion of the fifth nerve.

We may here consider two collections of nervous ganglia in the heart which are connected with the vagi and the sympathetic system. The two vagi pass to the sinus venosus and enter a nervous ganglion situated in its wall and known as **Remak's ganglion**. Thence the vagi pass into the auricular septum, one in its dorsal and the other in its ventral portion, and run backward to the region of the auriculo-ventricular groove where they enter another collection of nerve-cells known as **Bidder's ganglia**. From these ganglia fibres are distributed to the rest of the heart. These two minute collections of nervous matter are of importance to physiologists.

The eyeball of the frog is attached to the skull by muscles which have already been described. The eyeball is not spherical, but is flattened on its outer side, more convex on its inner side. It consists of the following parts: (1) a firm outer wall, the **sclerotic**, formed of cartilage and dense white connective tissue; (2) the **cornea**, a transparent area on the exposed part of the eyeball, through which light is admitted into its interior: it is continuous with the sclerotic; (3) a coloured curtain, the **iris**, lying behind the cornea, and surrounding a central aperture, the **pupil**. The iris is provided with circular and radial muscle fibres, by means of which the size of the pupil can be diminished or enlarged. In the interior of the eye a firm transparent spheroidal body lies behind the iris, attached to its outer margin. This is the **lens**, and it serves to focus light upon the back of the eye. Between the cornea and the lens is a small space, the anterior chamber of the eye, filled with a watery fluid, the **aqueous humour**. Between the lens and the back of the eye is a much larger space, the posterior chamber of the eye, filled with a gelatinoid material, the

vitreous humour. The sclerotic is lined by a black pigmented layer called the **choroid**, which is continued in front into the iris. Inside of this, lining the chamber of the eye, is a delicate transparent membrane, the **retina**, on which the ramifications of the optic nerve are spread. It is the sensitive portion of the eye, and the cornea, iris, lens, etc., are structures adapted to focus the light upon it.

The frog's ear is embedded in the periotic capsule, which, as we have seen, is largely cartilaginous, with an anterior ossification, the pro-otic. The essential organs of hearing are deeply

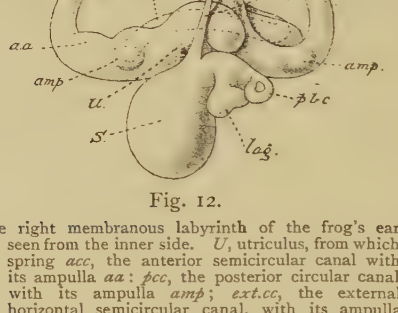

Fig. 12.

The right membranous labyrinth of the frog's ear seen from the inner side. *U*, utriculus, from which spring *acc*, the anterior semicircular canal with its ampulla *aa*: *pcc*, the posterior circular canal with its ampulla *amp*; *ext.cc*, the external horizontal semicircular canal, with its ampulla *amp*, represented as showing through the transparent walls of the utriculus; *S*, the sacculus; *de*, the ductus endolymphaticus; *lag*, lagena; *pbc*, pars basilaris cochleæ. (Adapted from Retzius.)

embedded in the cartilage, and only communicate with the surface by an accessory apparatus consisting of the **tympanic cavity**, the **eustachian tube**, and **columella**.

The tympanic cavity, bounded externally by the tympanic membrane, is seen, after removal of the latter, as a shallow, funnel-shaped cavity, lined by a pigmented mucous membrane, and communicating by the wide, short passage of the eustachian tube with the pharynx. The inner and deeper part of the cavity presents a small aperture leading into the inner ear. This aperture, called the **fenestra ovalis**, is blocked by the enlarged cartilaginous end of a partly bony, partly cartilaginous rod, the **columella auris**, which traverses the

tympanic cavity and is fixed by its outer end in the tympanic membrane. The tympanic cavity and eustachian tube together constitute the middle ear, and are derived from the most anterior of the gill-clefts of the tadpole. The inner ear consists of a membranous sac lying in a corresponding cavity of the cartilage of the auditory capsule. Between the cartilage and the sac is a fluid called **perilymph**. The sac also has fluid contents called **endolymph**. A constriction partly divides the sac into two portions: (1) an upper and larger division, called the utriculus; (2) a lower and smaller division, with three small dilatations on its posterior face, called the **sacculus**. The last named also gives off from its inner and upper border a tubular offset ending in a thin-walled dilatation. This is called the **ductus endolymphaticus**.

The utriculus has more complex relations. Three **semi-circular canals**, an anterior, a posterior, and an external, open into it. Of these the anterior semi-circular canal lies in the median or sagittal plane of the head; at its anterior end, just where it joins the utriculus, it is dilated to form an **ampulla**, and its posterior end joins the posterior semi-circular canal which opens, in common with it, into the utriculus. The posterior semi-circular canal lies in the transverse plane; its upper end opens into the utriculus, in common with the anterior canal, and its lower end dilates into an ampulla before opening into the utriculus. The external canal lies in the horizontal plane, and has an ampulla at its anterior end. Thus the three canals lie at right angles to one another in the three dimensions of space; they open into the utriculus at both ends, and each has an ampulla at one end. The auditory nerve, passing through an aperture in the inner wall of the auditory capsule, divides into branches, which are distributed to the utricle, the saccule, and the ampullæ. In the interior of the membranous labyrinth are the elements sensitive to sound-waves, in the form of modifications of the lining epithelium bearing stiff sensory hairs. There are also peculiar calcareous concretions, called **otoliths**, especially abundant in the ductus endolymphaticus.

The olfactory organs of the frog consist of a pair of sacs separated from one another by a median cartilaginous septum, and opening to the exterior by the anterior nares, into the buccal cavity by the posterior nares. The cavity of each

sac is divided up and complicated by the projection into it of cartilaginous offsets of the walls of the nasal chambers, and three main subdivisions or sinuses have been recognised in each sac—a dorsal, a ventral, and a lateral sinus. These sinuses are lined by an epithelial membrane which in the olfactory region is modified to serve as the percipient element.

We have thus far treated of the anatomy of the frog as it may be learned from simple dissection; and we have not, in dealing with the various tissues and organs, considered the ultimate elements of which these are composed. But we have already gathered important information respecting the plan of structure of the frog's body. We have seen that it has a special cavity, the **cœlom**, in which the abdominal viscera appear to be suspended, so we recognise the frog as belonging to the group **Cœlomata**. From its possessing a vertebral column with a central nervous tube placed dorsally to it we recognise it as being a **Vertebrated** animal; from its having a distinct head we recognise it as being a member of the **Craniate** branch of the vertebrata. As it has distinct jaws it must be placed among the **Craniata Gnathostomata**; and, as it has five-fingered arms and legs, and not fins, it must be a member of the sub-grade **Pentadactyla** of that group. Finally, the smooth glandular skin, the absence of nails or claws, the fact that it breathes when a tadpole by gills, when adult by lungs, show it to be a member of the class **Amphibia**.

CHAPTER III

THE HISTOLOGY OF THE FROG

We must now consider shortly the ultimate elements of which the complex mechanisms of the frog are built up, and we shall begin best by taking the simple case of the blood.

The blood differs slightly in colour according as it is taken from an artery or a vein. In the former case it is bright scarlet in colour, in the latter dark and almost purple in hue, but in both cases the microscopical characters are the same. The blood is an opaque viscid fluid, slightly alkaline in reaction, and consists of a fluid matrix, **the plasma**, in which solid particles of minute size, **the corpuscles**, are contained.

The plasma is a transparent fluid, of a pale yellow colour, containing albumens and some salts in solution. The corpuscles are of two kinds, red and white, and the white corpuscles may further be divided into three kinds. The **red corpuscles**, or **hæmatids**, are far more numerous than the white. Each is a flattened oval disc, measuring some 0·023 mm. in its widest and some 0·014 mm. in its shortest diameter; it is pale red or yellow in colour, and presents a central prominence due to the presence of a specialised central portion, **the nucleus**. If a film of blood is treated with certain dyes, such as carmine, hæmatoxylin (a preparation of logwood), magenta, etc., the flattened part or body of the corpuscle is but little affected by the stain, but the nucleus absorbs it readily, and may be seen to contain a network of a substance which stains more deeply than the rest. This intranuclear network, because of its strong affinity for certain colouring matters, is called **chromatin**. The body of the corpuscle may also be observed to be made up of a network of a denser substance containing a more fluid substance in its meshes. The red colour of the body of the corpuscle is due to the presence of an iron-holding compound named **hæmoglobin**, which can be separated out by shaking up blood with

ether. When separated, the hæmoglobin crystallises out in prisms. The hæmatids do not spontaneously alter their shape, but they are very elastic, so that they can easily be squeezed through passages smaller than themselves, and regain their shape after the passage, as may be seen in the capillaries of the frog's foot.

The white corpuscles or **leucocytes** are much fewer in number than the red, though their relative number varies con-

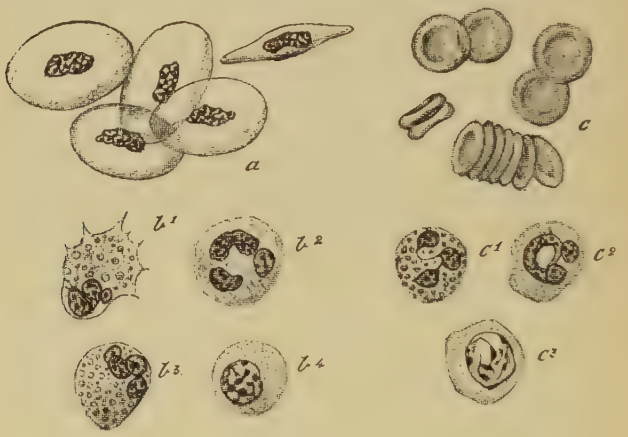

Fig. 13.

a, Red blood corpuscles (hæmatids) of the frog, stained with safranin and much magnified, to show the nucleus and nuclear network. *b1*, an amœboid coarsely granular leucocyte from the frog's blood, showing trifid nucleus; *b2*, *b3*, *b4*, other forms of leucocyte from the frog's blood. *c*, discoid non-nucleated hæmatids from human blood, much magnified; *c1*, *c2*, *c3*, different forms of leucocytes from human blood.

siderably in different individuals, and in the same individual at different times. A leucocyte, as it appears in freshly-drawn frog's blood, when viewed under the microscope, is a minute colourless body of smaller size than the red corpuscles, measuring some 0·017 mm. in diameter. It consists, like the hæmatid, of a protoplasmic body, containing a nucleus. The nucleus is not easily seen in a living corpuscle, but it becomes apparent on treatment with acetic acid, and it stains deeply with carmine and other colouring matters, whilst the protoplasmic body is

scarcely affected. Some of the leucocytes contain only a single nucleus, but, as a rule, they have two, three, or even four contained in a single protoplasmic envelope. The body of the leucocyte has no definite outer limiting membrane, and no constant shape. It usually contains granules of different kinds, and a few clear spaces called vacuoles, filled with fluid. Simple as its structure is, the leucocyte is living, endowed with the power of spontaneous movement, and capable of exhibiting by itself some of the fundamental properties of living organisms. In a sense a leucocyte may be said to be an independent organism, but its independence is not complete. It is incapable of separate free existence apart from the blood which forms its normal environment, and therefore we cannot isolate leucocytes, and study them apart from the blood, and deal with them as independent living beings. But within the blood as it courses through the tissues, or in blood freshly drawn from the body, the leucocyte behaves as a separate organism complete in itself. That it is contractile, and capable of change of shape, is easily seen on simple inspection of a sample of freshly-drawn blood. The leucocytes do not remain still, nor do they retain a constant form as do the hæmatids, but are continually in movement, putting forth irregular blunt processes of their protoplasm in various directions, and again withdrawing them. These blunt movable processes are called **pseudopodia**, and the movement due to them, from its resemblance to that of a minute organism, the Amœba, which we shall study presently, is called **amœboid**. That the leucocytes are "automatic"—that is to say, endowed with the power of spontaneous movement—is shown by their constant changes of form; changes which, so far as can be determined, are called forth by no definite external stimulus. But the corpuscle is also irritable; for if the blood be very gently warmed the activity of the pseudopodial movement is increased; if the temperature be much lowered it will be decreased or stopped altogether, to recover when the temperature is raised again. Certain drugs also, such as quinine, retard the activity of the leucocytes. The leucocytes are assimilative, for they surround and take into their bodies foreign substances; many of them are seen to be filled with fat granules, and it has been shown that these are ingested, swallowed, as it were, during the passage of the blood through the intestine. And leucocytes

ingest many other substances such as bacteria, this phenomenon being known as **phagocytosis**. The fat granules may be subsequently extruded from the corpuscle, or they may be used up and converted into its substance, and therefore the leucocyte is assimilative and metabolic; for, although we cannot measure the expenditure of energy nor trace the formation and rejection of waste material in so small a body, we are certain that the exhibition of energy in the form of pseudopodial movement must involve a chemical change; a decomposition of the chemical substances of which the corpuscle is composed, and the production of waste matters as a result of the decomposition. And the leucocytes are reproductive, for they may be observed to divide into two, each portion containing a part of the nucleus, and the daughter leucocytes thus formed carry on the existence of the parent form which gave origin to them, and lead independent existences as individual leucocytes. In short, the leucocyte manifests all the activities characteristic of a living being, and withal it is nothing more than a speck of that peculiar life-substance which we call **protoplasm**, showing scarcely any structure, beyond that it is divisible into nucleus and cell-body —for the leucocyte is a fairly typical example of what is called a **cell**; and, before we consider the different kinds of leucocytes which occur in the blood and lymph of a frog, we may pause for a moment to consider what a cell is.

"A cell is a corpuscle of protoplasm which contains within it a specialised component particle, the nucleus." Such is the definition of a cell given by one of the most notable living authorities on the subject, and for our present purposes the definition may be accepted. But it must be remembered that it is well-nigh impossible to frame satisfactory definitions concerning living things. "A cell is a corpuscle of protoplasm containing a nucleus." But we have just seen that a leucocyte, a single corpuscle of protoplasm, may contain two or more nuclei. Is it still a cell? or, does the increase of the number of nuclei remove it from our definition? In the case of the leucocyte, certainly not. The double, treble, or quadruple nucleus is clearly brought about by division of a single nucleus, and the parts are smaller than the whole from which they were formed. And it appears that when a multinuclear leucocyte reproduces itself by division each nuclear

fragment does not divide prior to the division of the cell-body, so that the new daughter cells shall contain as many nuclei as there were in the parent cell, but that a half of the nuclei pass over to one cell, the other half to the other cell formed by division. Moreover, the occurrence of truly multinucleate leucocytes is much rarer than is commonly supposed; for, even where two or three nuclei seem to be present, close inspection reveals the fact that they are united together by strands of nuclear substance. In fact, the nucleus of the leucocytes is rather irregular and lobate than divided into separate portions, and it is the irregular lobes folded over one another which give the appearance of several nuclei. Such irregular nuclei are in other respects similar to normal spherical or sub-spherical nuclei; they contain a network of the deep-staining substance, chromatin, and in division behave as do ordinary nuclei.

But, as we shall see farther on, there are many unequivocal instances of numerous independent nuclei being enclosed in a single mass of protoplasm. Some authors regard these as single cells, because the protoplasmic mass, the cell-body, is single. Others hold an opposite opinion, and it is not an easy matter to decide which of the two opinions is to be preferred. But, as a matter of convenience, it is well to call a single mass of protoplasm containing more than one nucleus by a special name—viz. **cœnocyte.**

We have said that a cell consists of a mass of protoplasm containing a nucleus. But this is not a satisfactory definition; for protoplasm is a vague general term which at the present day has no very exact meaning attached to it. Protoplasm, the material basis of life, was first discovered by Dujardin, who called it **sarcode**. Dujardin stated precisely what he meant by sarcode. "It is that," he said, "which other observers have called a living jelly—that gelatinous, diaphanous structure, insoluble in water, which contracts into globular masses, attaches itself to one's dissecting needles, and can be drawn out in strings like mucus." Further than this, Dujardin recognised that sarcode must be **organised**, must possess a structure. Not that he was able, with the imperfect microscopes of the day, to observe and describe a structure, but he felt bound to postulate one, because of the vital activity of the substance. "Sarcode is without visible organs, and without the appearance

of cellulosity, but it is nevertheless organised, since it emits diverse prolongations carrying granules with them, extending and retracting themselves alternately—in a word, it has life."

The word "protoplasm" is due to a botanist, Hugo von Mohl, who, in 1846, described the constitution of the so-called primordial utricle in plant cells—a semi-fluid, gelatinoid, living substance, similar to the sarcode already described by Dujardin. But, curiously enough, the identity between the sarcode of animals and the protoplasm of plants, does not seem to have struck the physiologists of the time. One distinguished anatomist, Robert Remak, did indeed perceive the identity between them, and applied the term protoplasm to the substance composing animal cells, but his example was not generally followed, and it was not until 1861 that the modern conception of protoplasm was expounded by Sigismund Max Schultze, to whom also we owe the definition of a cell as given above—"a corpuscle of protoplasm within which lies a nucleus" (Ein Klümpchen Protoplasma, in dessen Innerem ein Kern liegt).

Max Schultze showed by means of many beautiful and convincing experiments, the identity in the behaviour of the protoplasm of plants and animals; that both consist of a hyaline, contractile, jelly-like ground substance containing minute granules; that in both animals and plants the granules may be seen to be in constant movement, streaming in definite courses through the ground substance; that the effects of heat, electric stimulus, and chemical action are the same in plant as in animal protoplasm.

But still the term protoplasm has remained vague, and several rival theories as to its constitution have been put forward. The name itself has become too general, and though it remains in use, it is on the tacit understanding that it means the substance of the cell-body of such primitive cells as we call undifferentiated. The cell-body of the leucocyte is a good instance of what is meant; but nowadays it is usual to refer to the material of the cell-body as **cytoplasm**, and to that of the nucleus as **nucleoplasm**, it being understood that neither of them are homogeneous chemical compounds of definite formula, but mixtures of several different kinds of albuminous bodies, each of great molecular complexity.

We may regard the terms "protoplasm" and "cytoplasm"

as being nearly synonymous, the former having a slightly wider and more general meaning than the latter.

The ultimate structure of protoplasm, as far as it can be determined by the best modern microscopes, is comparatively simple and gives no clue to the wonderful vital properties manifested by living cells. The cytoplasm of an undifferentiated cell, such as a leucocyte, appears as a network, or rather a sponge-work, of a denser albuminous material holding a more fluid substance in its meshes or cavities. The granules so generally present in the cytoplasm are of various kinds; they may simply be substances taken into or elaborated by the cell; or they may be proteid bodies of more complex constitution, multiplying by division and behaving like miniature cells within the cell. In the latter case they are distinguished as plastids. The nucleus has a more complicated visible structure and chemical constitution than the cytoplasm, as is shown by its behaviour towards staining fluids and other reagents. Externally, separating the nuclear contents from the surrounding cytoplasm is a **nuclear membrane**. Within the membrane is a network or sponge-work of fine fibrils, composed of a substance called **linin**, holding a semi-fluid matter in its meshes. As the fibrillar network does not stain readily with the usual dyes it is known as the **achromatic network**. The most obvious and in some respects the most important constituent of the nucleus is a deeply staining substance called **chromatin** which, in the normal resting condition of the cell, is scattered in the form of granules along the achromatic network and therefore appears itself to have a reticular arrangement. The nucleus may also contain a spherical body, the **nucleolus**, which stains as readily as the chromatin but in a different manner, and is composed of a chemically different substance called **plastin**. Chromatin is a compound of a highly phosphorised organic acid—**nucleic** acid—with albumen. The cell, then, has an organisation, a complex constitution, such as Dujardin postulated for his sarcode. It consists essentially of a cell-body or cytoplasm and a nucleus, and both cytoplasm and nucleus are mixtures of several very complex chemical compounds whose formulæ have not yet been worked out.

It is clear that both kinds of corpuscles contained in the frog's blood, the hæmatids and the leucocytes, are cells. Both have a cell-body and a nucleus, yet they differ in a marked

degree from one another. The leucocyte is comparatively formless, and its characters are such as to afford an excellent illustration of what we mean when we speak of an animal cell. It is, in fact, an embodiment of our idea of a cell, and is therefore what we call typical or generalised. The hæmatid, on the other hand, has characters all its own. Its structure departs from the general conception, because it is altered in connection with its function as a carrier of hæmoglobin, and it is what we call specialised or differentiated. Its cell-body is not simple protoplasm, but is in large part changed into something that is not protoplasm but has been formed by or out of protoplasm. This circumstance shows us that a cell has activities, that its constituent protoplasm has the power of changing itself into some special substance, or of manufacturing some special substance, and depositing it within the limits of the cell. A cell, therefore, has formative powers, in virtue of that mysterious attribute of its constituent protoplasm which we call life. Life is the sum-total of the activities of the cell.

The truth of this statement is borne in upon us when we examine further the constitution of the other tissues of the frog's body. All of them, skin, bone, cartilage, nervous tissue, muscular tissue, gland tissue, are formed either of cells, or of the union of the products of cells. But there are few of the constituent cells of the frog's body which are as simple and generalised as the leucocytes of its blood.

We may first of all study the composition of the membranes which cover the surface or line the cavities of the body. These are called **epithelia**; and, since all epithelia are composed of cells, the latter are known as epithelial cells. The most simple kind of epithelium is perhaps that variety known as **columnar. Columnar epthelium** is found in the intestine of the frog, lining its cavity, and forming the coverings of the minute processes, called villi, which project into the cavity. Each component cell of a columnar epithelium is a prism of greater or less height, the body of the prism being cytoplasm, in the interior of which lies a nucleus. These prismatic cells usually rest on a very fine basement membrane, which is not cellular, but produced by the cells. The prisms form a single layer, are pressed close together, and owe their prismatic shape to mutual pressure. They are not so closely packed, however, but that there are minute intercellular spaces

between adjoining cells, and these spaces, which communicate with the lymph system, are generally traversed by exceedingly fine protoplasmic fibrils passing from cell to cell, and so establishing protoplasmic continuity throughout the whole tissue. But, in spite of this protoplasmic continuity, we recognise that the tissue is not a single tract of protoplasm containing many nuclei, but is really composed of individual cells, just as we should recognise that a house is really composed of a number of rooms, though they all communicate by means of doors. Columnar cells may be tall and thin, or short and broad, or mid-way between these two extremes. Their nuclei are usually placed mid-way between their free ends and their bases.

Such cells as those just described are simple columnar epithelial cells; but there are many varieties of columnar epithelium. One of the most common of these is **ciliated columnar epithelium**, to be obtained from the frog's palate, or, better, from the windpipe of higher vertebrates, or from the gills of such a mollusc as the fresh-water mussel or the oyster.

If a minute scraping be taken with the point of a knife from the roof of the buccal cavity of a freshly-killed frog, and the whitish material thus obtained be mounted on a glass slip in a ·75 solution of common salt and examined under the microscope, it will be seen to consist of a number of translucent rounded cells, in most of which a large nucleus can be seen. There are several kinds of these cells, but some of them are conspicuous because of a continual shimmering movement on one of their surfaces; if such a cell be isolated from the remainder of the mass it will be seen to gyrate and spin round and round in the salt solution. After some time the movement becomes slower, and then it can be seen that the cell bears on one surface a tuft of very fine, hair-like transparent processes of highly contractile protoplasm, called **cilia**. When the movements have slowed down, it may be seen that the cilia work in unison, with a sort of lashing movement, bending very sharply in one direction, and then more slowly relaxing till they regain their straightness, when they again bend sharply as before. Tracts of these cells cover the frog's palate, and their cilia, by their united action, drive mucus and small particles of foreign matter along in a given direction. If the ciliated cells are killed by a drop of very

dilute osmic acid, and afterwards stained with carmine, they are seen to be shaped like those represented in fig 14, *D*. Each cell is shaped like a truncated club; its broader end is turned outwards, and its edge is formed by a border of highly refracting contractile substance differing in appearance from the cytoplasm of which the rest of the cell-body is composed. From this border the cilia project into the cavity of the pharynx. The cell tapers gradually inwards, its inner end being fine and pointed or drawn out into two or more irregular processes which rest upon a basement membrane. The nucleus is relatively large, placed in about the middle of the length of the cell, which is rather bulged out by it. The ciliated cells found on the gills of oysters and mussels are larger and have longer cilia than those of the frog's palate, and afford a very convenient means of studying ciliary action. The great, flat, plate-like gills of these animals are covered with a ciliated epithelium, whose cilia, constantly in motion, drive currents of water through the gills in a definite direction. The cells are long and columnar, tapering internally, and with large nuclei. The refracting border on the free surfaces of the cells may be seen to be made up of a number of minute refractive knobs placed close together. Each knob bears a cilium on its outer side, and internally it is prolonged into a fine varicose fibril which runs down into the cell-body past the nucleus, eventually uniting with similar fibrils from the other knobs to form a single thread which runs into the pointed inner extremity of the cell (fig. 14, *D* 3).

Several phenomena may be noticed in a fragment of the gill of an oyster or mussel examined under the microscope. The ciliary motion appears to sweep over the surface in waves, just as a field of corn is thrown into waves by the wind passing over it, and the waves always pass in the same direction. The ciliary motion continues for some considerable time in the excised piece of gill, and even in small fragments or single cells which have been broken away with needles. This shows that the activity of the cilia is not due to impulses reaching the cells by nerves from the nervous centres, but that it is dependent on the activity of the cells themselves, which remain living for some time after their removal from the body. If the temperature is lowered the activity of the cilia is diminished, and eventually is stopped altogether at some

degrees below freezing point, but it is revived on warming. Up to a certain point warmth increases the activity of the cilia, but above a certain point it retards, and soon stops their motion altogether. The cilia pass into a stiffened condition, known as heat rigor, from which they do not recover. In warm-blooded animals the optimum temperature for ciliary motion is about 45 deg. C. In cold-blooded animals the temperature of the body appears to be the optimum, but as this varies according to the temperature of the surrounding medium, we find the cilia more active in summer heat than in winter cold. Oxygen, at least in its free state, is not essential to the action of cilia, as may be shown by the fact that it will go on for some time in water, which has been deprived of all its dissolved oxygen by boiling. This experiment, however, does not prove that the source of energy is anything else than the oxidation of the substance of the ciliated cells, but rather that the cells can store up oxygen in a combined form for use when required. Carbonic acid gas has a definite effect in arresting ciliary motion, as can be seen if a stream of the gas is passed over a preparation of active ciliated cells. Their motion is at first accelerated, but soon slows down, and may be arrested altogether. It soon is restored, however, on the readmission of fresh air. Chloroform vapour acts in the same way as carbonic acid gas. Ciliated cells are found in various parts of the frog's body: in the pharynx and olfactory passages; on the edges of the partitions separating the alveoli of the lungs; in the central canal of the spinal cord, and the ventricles of the brain; in the uriniferous tubules of the kidney, and in the ureters; in the oviducts, and, in the tadpole, on the epithelium covering the transitory gills.

Both columnar and ciliated epithelia belong to the variety of epithelium known as simple, because their component cells are arranged in a single layer. Another variety of simple epithelium is that forming the thin membranes lining internal cavities, such as the cœlom, the heart and blood-vessels, the lymph-spaces, etc. This variety is often referred to under the name **endothelium**, but may more conveniently be described as **pavement** epithelium. Pavement epithelium may be very advantageously studied in the mesentery of the frog. Both sides of the mesentery are covered with a very thin membrane continuous with that lining the pleuro-peritoneal cavity. This

membrane is composed of very thin, flat, scale-like cells, which may be polygonal, and fit together by their edges, like the tiles in a pavement, but more usually have serrated or sinuous edges which dovetail into one another, like the wooden puzzles of children (fig. 14, *B*). Each scale-like cell has a distinct nucleus which bulges out its central portion. In order to see

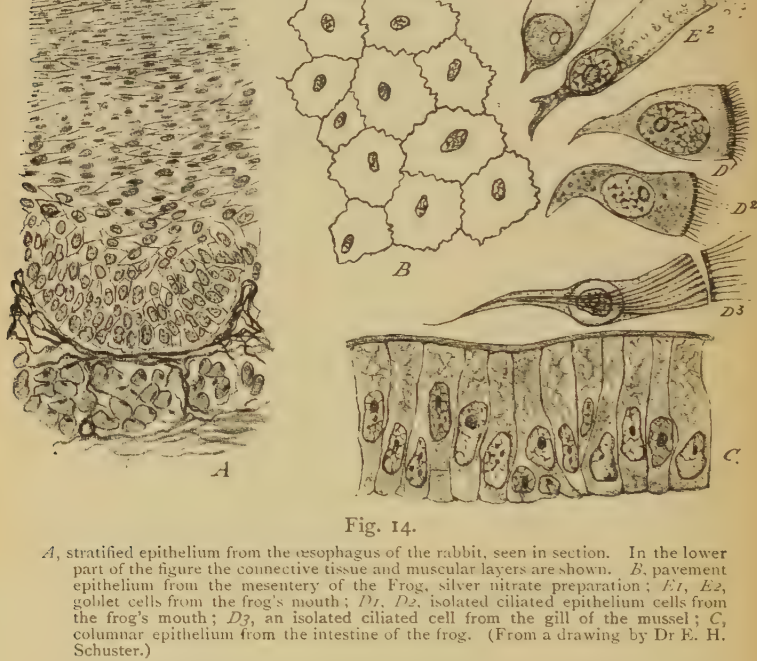

Fig. 14.

A, stratified epithelium from the œsophagus of the rabbit, seen in section. In the lower part of the figure the connective tissue and muscular layers are shown. *B*, pavement epithelium from the mesentery of the Frog, silver nitrate preparation; *E1*, *E2*, goblet cells from the frog's mouth; *D1*, *D2*, isolated ciliated epithelium cells from the frog's mouth; *D3*, an isolated ciliated cell from the gill of the mussel; *C*, columnar epithelium from the intestine of the frog. (From a drawing by Dr E. H. Schuster.)

the outlines of pavement-epithelial cells it is necessary to treat the membrane with nitrate of silver and expose it to the light. The intercellular substance between the cells has the property of being able to reduce the nitrate in the sunlight, and is accordingly filled with particles of metallic silver, which mark out the outlines of the cells in black.

Stratified epithelium is distinguished from simple by the fact that its component cells are arranged in several layers or strata, it is commonly said like a heap of tiles; but the simile is not exact, for the tiles at the bottom of the heap would have to differ from those at the top to make the comparison good. Stratified epithelium is found in the epidermis or outer skin, the cornea, and other parts of the frog. In the epidermis there are several layers of epithelial cells; the lowest are more or less columnar in form, arranged in a definite row, and have abundant cytoplasm in the cell-body: this layer is commonly known as the **stratum malpighi**. The cells of the middle layer become progressively more flattened and polygonal in outline, and the outermost layer consists of quite flat transparent scales, in which the nucleus is still present, but the cell-body has been converted into a horny substance. The skin of man is formed of a somewhat similar stratified epithelium, with a more abundant horny outer layer; this extends into the mouth, and it is easy to scrape some of the superficial layer from the roof of one's mouth, and observe the horny scales of which it is composed. The epithelium lining the urinary bladder of the frog (and of mammals) presents a variety intermediate between columnar and stratified epithelium. There are three layers of cells, but they do not over-lap one another, nor are those of the outer layer horny and flattened; they are dovetailed together by their wedge-shaped and serrated upper and lower ends, those of the outermost layer, lining the cavity of the bladder, being almost columnar in form. This is known as **transitional epithelium.**

Both in the epidermis and in the alimentary canal of the frog there are numerous glands of simple structure; and the liver and pancreas are large glands of more complicated structure. The essential part of these glands is the epithelium lining their cavities, its cells being modified to form what is known as **glandular epithelium**. There are also many uni-cellular glands amongst the columnar and ciliated cells in the buccal cavity, and amongst the stratified cells of the epidermis. Excellent examples of these single gland-cells are to be found amongst the ciliated cells scraped from the palate. Each has the form of a modified columnar cell with a broad free extremity and a narrow fine-pointed internal extremity. The **goblet** or **chalice-cell**, as it is

called, elaborates a substance by the activity of its protoplasm, obtaining the necessary material from the blood, or rather from the lymph which surrounds it. This substance (which in the case of the chalice-cells of the palate is **mucus** or slime) is called the **secretum**, and is stored up in granules in the distal end of the cell between its nucleus and its free border. When secretion takes place, the free wall of the cell bursts, and the secretum is poured out; the cavity which it occupied in the distal end of the cell remains as a hemispherical cup, which, situated as it is on the attenuated inner extremity, gives the whole cell the appearance of a goblet (fig. 14, *E*). After secretion, the protoplasm of the cell again enters into activity, and a fresh secretum is produced, to be discharged in due course. The simplest kind of multi-cellular gland is found in the stomach and intestines of the frog and other vertebrate animals. The mucous membrane lining these organs, when examined superficially with a microscope, is seen to be pitted with innumerable minute orifices placed close together. These are the mouths of simple tubular glands, each of which has the form of a shorter or longer tube formed as a finger-like recess in the connective tissue layer or **corium** underlying the epithelium of the alimentary tract. These tubes, which are longer in the stomach and shorter in the intestine (in this last situation they are known as the crypts of Lieberkühn), are lined within by an epithelium, which is a continuation of the columnar epithelium lining the cavity of the alimentary tract. At the mouths of the glands the cells are high and columnar, having the same characters as those lining the cavity of the gut. In the next section of the gland, known as the **neck**, the cells become progressively shorter and more cubical, and in the deeper part of the gland they become larger and polyhedral, and change their character, in that they have contents in the shape of numerous granules, most abundant in the ends turned towards the lumen of the tube. The opposite ends of the cells are formed of ordinary cytoplasm, and the nucleus lies in the borderland between the granular and the protoplasmic part. The granules are the secretum of the cell, and are formed by the activity of its protoplasm. They are, however, not considered to be the actual secretum, but rather a precursor of the secretum peculiar to the cell; and, as the cells of the gastric glands

secrete a **ferment** or **enzyme**, the granules which are the precursor of that ferment, are called **zymogen** granules. When secretion takes place the granules are discharged from the cells into the lumen of the gland, become converted into ferment, and this is poured into the cavity of the gut. Amongst the gland-cells of the frog's stomach mucus-secreting chalice or goblet cells are found. In the pyloric end of the frog's stomach the cubical epithelium is continued nearly down to the blind end of the gland, its terminal portion only being occupied by a few large gland-cells filling up its cavity.

In the mammalian stomach the simple tubular glands are slightly complicated by the branching of their extremities, so that two or more tubes open into a single short neck or duct, and in the cardiac end of the stomach the glands have two kinds of cells in the walls of their deeper portions, **chief cells** in the form of normal gland-cells, and **parietal cells**, which are ovoid, filled with darkish granules, and lie between and behind the chief cells, between them and their basement membrane. The chief cells secrete the digestive fluid pepsin, the parietal cells secrete the acid (hydrochloric) found in the gastric juice, and hence are also known as **oxyntic** cells.

Such glands as the pancreas, or the salivary glands of mammals, are of the kind known as **racemose**. They may easily be derived from the branched tubular condition of the gastric glands, by supposing the branches of the latter to divide and sub-divide, the proximal portions of the duct and branches being lined by simple non-glandular cubical epithelium whilst the distal end are dilated to form the so-called **acini** lined by glandular cells. The whole structure is called racemose from its resemblance to a bunch of grapes, the stalk and its divisions being the ducts, the grapes the secreting portions or acini.

In the case of the liver the bile-ducts are lined with a columnar epithelium which changes as the ducts break up into finer and finer ramifications, the columnar cells passing insensibly into the hepatic cells, whilst the cavities of the ductules become no more than irregular spaces running between the liver-cells, and are known as **bile-capillaries**. The hepatic cells form the bulk of the liver; they are large, polygonal in shape, and possessed each of a single nucleus. These liver-cells, especially if taken from an animal killed not long after a meal, may be seen to contain numerous granules

composed of the carbohydrate called **glycogen**. Glycogen is a substance belonging to the group of Amyloses or starches [formula $(C_6H_{10}O_5)_n$]. It gives a port-wine red colour with iodine, and the granules may easily be stained with this reagent in fresh liver-cells.

In certain parts of the body individual epithelial cells are modified in connection with sensory surfaces. Such modified epithelia are known as sensory or **neuro-epithelia**, and the cells composing them may conveniently be described as **end-cells**. They are found in the frog in the forms of **taste-cells** on the tongue and palate, **olfactory cells** in the olfactory region of the nasal cavities, **rods** and **cones** in the retina of the eye, **hair-cells** in the labyrinth of the ear, especially in patches on the ampullæ of the semi-circular canals, and **touch-cells** on the touch-spots of Merkel, which are best seen on the swelling on the thumb of the male during the breeding season. There are also end-cells in the sense organs of the lateral line, highly developed in the tadpole, but degenerate in the adult frog.

We may take the olfactory cell as a good example of a neuro-epithelial cell (fig. 15, *D*). In the olfactory region of the nasal chamber the epithelium is mostly composed of columnar epithelial cells, produced internally into long branched processes. Amongst these are placed cells, each of which possesses an ovoid body enclosing a large nucleus. From the body a peripheral or distal and a central or proximal process is given off. The former reaches the surface of the surrounding epithelium, and bears at its end a few (5 to 8) stiff hair-like processes, which may be modified or fused cilia, but, unlike cilia, are immovable. The central process of the cell consists of a very fine varicose fibre, which passes into a sub-epithelial plexus composed of similar fibres from other olfactory cells and the inner branched ends of the epithelial cells. Each fibril of an olfactory cell is continued into a fibril of the olfactory nerve.

The rods and cones of the retina are peculiar structures, each being a product of rather than a metamorphosed epithelial cell. A rod is a cylindrical rod-shaped body about 0·05 mm. in length, consisting of two parts, a longer, highly refractive, outer limb, and a shorter, more homogeneous, less refractive, inner limb, separated by a small plano-convex

structure known as the **lenticular body** (fig. 15, *C*). At the base of each rod is an oval nucleus surrounded by a very thin sheath of granular protoplasmic matter which is continued internally as a fine fibril; this probably becomes continuous with, or comes in contact with, a terminal fibril of the optic nerve.

Hair-cells from the crista acustica of an ampulla of the ear

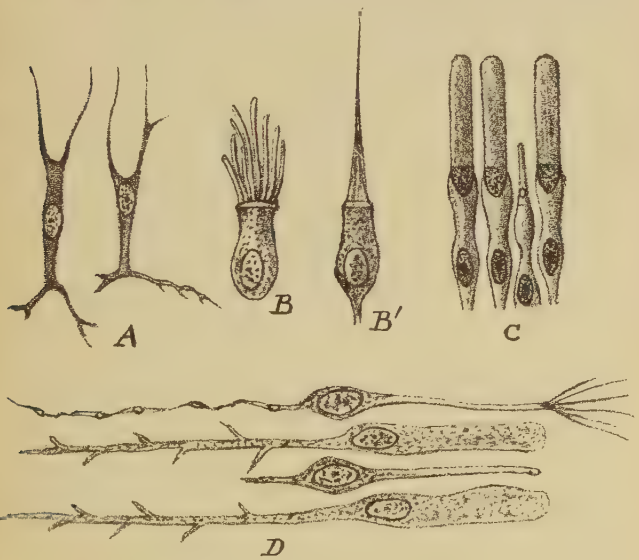

Fig. 15.

Various forms of sensory epithelium. *A*, two forked cells from the tongue of the frog; *B*, *B′*, two forms of auditory hair cells from the crista acustica of the anterior ampulla of the frog's ear; *C*, three rods and a cone from the retina of the frog's eye; *D*, two olfactory cells, with their epithelial supporting cells from the frog's nose. (All the figures after Haslam in Ecker's "Anatomy of the Frog." Engl. Ed.)

are shown in fig. 15, *B*. Each is a pyriform cell, the narrower end turned towards the cavity of the ampulla, and bearing on its truncated free surface a long stiff hair-like process which rests by a broad base on the cell. The opposite broader end of the cell usually appears rounded, but sometimes a fine fibril may be seen springing from it, and this probably becomes continuous with a terminal fibril of the auditory

nerve though the connection has not actually been traced. The characters of taste-cells may be learned by an inspection of fig. 15, *A*.

It should be noticed that epithelia play a very important part in the economy of the animal, and that the cells of the outer skin, as well as those lining the gut, are modified in diverse ways for the performance of diverse functions. The endothelia lining the cœlom, the cavities of the heart and blood-vessels, the lymph-spaces, etc., must be considered as belonging to a different category from the other two epithelia, since they are formed from the middle of the three embryonic layers, and are differentiated in one respect only—viz. in respect of their function as components of a limiting membrane.

In the nervous system of the frog two principal elements are to be distinguished, **nerve ganglion cells** and **nerve-fibres.** The former are found in the cortical substance of the brain and in the so-called grey matter surrounding the central canal of the spinal cord and forming the floor of the fourth ventricle in the medulla oblongata. They are also found in the various ganglia which have been described; such as the ganglia of the dorsal roots of the spinal nerves and the sympathetic ganglia. Nerve ganglion cells, however, may most easily be studied in the spinal cord of a larger animal, such as the ox. In that part of the grey matter known as the anterior horn of the spinal cord a few large cells may be seen in transverse section or may be separated by suitable methods of maceration. Each ganglion cell has a body composed of a finely granular cytoplasm, which sometimes appears to be indistinctly striated or reticular in structure. In the centre of the cell-body is a nucleus, which usually has the form of a relatively large, clear, rounded vesicle with a distinct nucleolus. The intra-nuclear network of chromatin is not usually well defined. The most characteristic feature in a nerve-cell is the prolongation of the cell-body into long branching processes, which show a distinct but fine longitudinal striation, the striæ of one process being continued over the peripheral parts of the cell-body to unite with the similar striæ of an adjacent process. A nerve-cell from the anterior horn of the spinal cord of the ox or other mammal has numerous processes (see fig. 16, *A*), which break up into branches at a little distance from the cell-body, and the

branches sub-divide again till they end in very fine nerve-fibrils, which inosculate with fibrils from adjoining cells. One process, however, is not branched, and may be traced into direct continuity with the axial fibre of an efferent nerve of the ventral root. The nerve-cells of the anterior horn are large, and are called multi-polar because of their numerous processes, but nerve-cells from other parts may be much smaller, and may vary both in the number and the mode of attachment of their

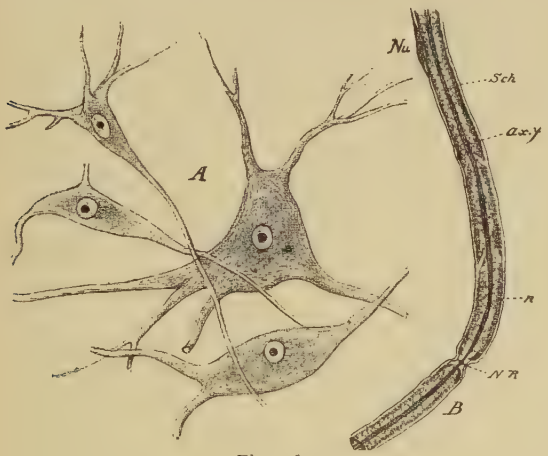

Fig. 16.

A, multipolar nerve ganglion cells from the spinal cord of an ox; *B*, portion of a medullated nerve fibre from the sciatic nerve of the frog, highly magnified; *a.x.f*, axial filament; *N R*, Node of Ranvier; *n*, neurilemma; *Sch*, medullary sheath or white sheath of Schwann; *Nu*, nucleus. The preparation was treated with osmic acid, which blackens the medullary sheath, and the breaks in its continuity as shown in the figure are probably due to the action of the reagent.

processes. Thus there are bi-polar nerve-cells with two processes, or uni-polar cells with one process only; and in the superficial layer or cortex of the cerebellum of mammals there are remarkable ganglion cells, called the corpuscles of Purkinje, having a pyriform body, produced at the narrow end into one or two stout processes, which immediately branch and break up into a number of fine fibres, running with more or less straight courses towards the surface of the cortex. The

broad end of the cell is usually produced into a single fine fibril. A curious form of nerve-cell is found in the sympathetic ganglia of the frog and of mammals. The cell-body is pear-shaped and enclosed in a distinct sheath. From its narrower end two processes are given off, of which one, the larger, starts from the deeper part of the body of the cell and pursues a straight course, being, in fact, the direct continuation of a nerve-fibre. The second smaller fibre starts from a plexus of fine fibrillæ on the surface of the cell-body, and is wound spirally round the larger fibre, eventually quitting it and taking an opposite course.

Nerve-fibres are of two kinds, **white** or **medullated nerve-fibres**, and **grey** or **non-medullated nerve-fibres**. The latter are chiefly found in the sympathetic system, but also occur, though not abundantly, in the cerebro-spinal nerves. They are transparent fibres with a faint longitudinal striation, and exhibit nuclei at frequent intervals on their courses. It is doubtful whether the nuclei lie outside the fibre, enclosed in a delicate investing sheath, or whether they are embedded in the superficial layer of the fibre itself.

White medullated nerve-fibres form the bulk of the white matter of the brain and spinal cord, and of the cerebro-spinal nerves. They are called "white" because, shortly after death, a peculiar fatty substance forming their sheaths sets hard and white, but during life it is liquid, and the fibres have then a pale transparent aspect. A single white fibre may be roughly compared to an insulated telegraph wire. The transmitting part, the actual wire, is represented by a pale strand of tissue, having the characters of a non-medullated fibre, and known as the **axial fibre** or **axis-cylinder**. It is nearly certain that every **axis-cylinder** is a direct prolongation of a process of a nerve ganglion cell, and it is to be remarked that the axis-cylinder of a nerve-fibre runs an uninterrupted course from the nerve-cell from which it originates to its peripheral termination. The insulating gutta-percha sheath of a telegraph wire is represented in the nerve fibre by a sheath of a **medullary substance**, or **myelin**, composed chiefly of the peculiar phosphorised fat, **lecithin**, and the calico or canvas outer wrapping of the telegraph wire is represented in the nerve-fibre by a delicate external homogeneous covering, called the **primitive sheath of Schwann**, or the **neurilemma**.

The neurilemma forms a continuous covering to the nerve-fibre, but the medullary substance is broken up into segments by constrictions, placed at regular intervals, and known as the **nodes of Ranvier**; and, in this respect, and in others, the simile of the telegraph wire will help us no further. Each node of Ranvier is formed by a constricting band, in the form of an annular ring extending inwards from the neurilemma to the axial-fibre. The nature of this constricting band is not very well understood, but its staining properties suggest that it belongs to the class of intercellular substances, and if this view be correct each internode would appear to be formed as a single cell. This view is strengthened by the fact that in each internode there is a single nucleus, surrounded by a small quantity of granular matter, and lying underneath the neurilemma, between it and the medullary sheath. But the axial-fibre is continued without interruption across each node of Ranvier, and it has been shown, both in development and in the regeneration of a nerve-trunk which has been divided, that the axial-fibre, which we must regard as the essential part of a medullated nerve-fibre, is formed as an outgrowth of a nerve-cell, and is therefore to be regarded as a very much elongated process of a nerve-cell, and not as a product of a number of cells represented by the nuclei of the internodes. This much, at any rate, is certain: that every nerve-fibre, continuous as it is with a process of a nerve-cell, is dependent on that cell for its nutrition, and dies if it is divided off from the cell. It is furthermore certain that, in the course of development, nerve-fibres first appear as pale fibres, destitute both of medullary sheath and neurilemma. The next thing to make its appearance is the neurilemma, which is nucleated, and is known at this stage as the nucleated sheath of Schwann, and lastly, the medullary sheath makes its appearance comparatively late in embryonic life. It is supposed by some authorities that the medullary sheath is formed by the activity of the cells composing the nucleated sheath of Schwann, and that, in the adult nerve-fibre, the medullary sheath and neurilemma of each internode represent the results of the activity of a single cell derived from the nucleated sheath of Schwann, whilst the axial-fibre which they surround is something different—namely, a process of the nerve-cell proper to the fibre. Other authors, however, hold that the medullary sheath is formed from the

axial fibre, and the neurilemma alone from the nucleated sheath of Schwann ; and the phenomena of regenerating nerve-fibres certainly lend support to their view. The subject is complicated, and cannot be profitably discussed in this place ; but it is important to remember, firstly, that the axis fibre is an outgrowth from, and is nourished by, a nerve-cell ; secondly, that the nodes of Ranvier mark off the limits of cells which have become secondarily related to the axis fibre, and are represented by the nuclei found in each internode. It may remain an open question whether the cells in question form both medullary sheath and neurilemma or the latter only.

A further peculiarity may be mentioned, that in most preparations the medullary sheath is seen to be broken up into segments, with conical or funnel-shaped ends which fit into one another. There may be many such in a single internode, and it is a moot point whether they exist in the living nerve or whether they are the result of post-mortem changes, induced perhaps by the reagents used in the preservation of the nerves. Towards their terminations, both afferent and efferent nerves lose their medullary sheath, and the axis cylinder breaks up into minute ramifying fibrils which exhibit characteristic varicosities. These terminal ramifications are distributed in various ways ; as, for instance, over the surface of a muscle in the case of efferent nerves, or a fibril may be continuous, as we have seen, with internal process of a sense-cell, in the case of afferent nerves.

The nervous tissues are the eminently irritable, the muscular tissues the eminently contractile. Muscular tissue is of two kinds, **plain** or **non-striated**, and **striated** or **striped** muscle. The latter presents two important varieties : the one found in the heart is known as cardiac muscular tissue, the other forms the skeletal muscles. As plain muscle-fibre is usually removed from the control of the will it is also called **involuntary**, and the striped muscle, being under the control of the will, is called **voluntary** ; but these names are not satisfactory, since cardiac muscle, though striated, is involuntary.

Plain muscular tissue (fig. 17) is found in the walls of the alimentary tract, in the walls of the arteries and veins, in the bladder, and in other viscera. It may occur in bundles or in layers, and is formed of distinct cellular elements, which may be separated from one another by suitable methods. A plain

muscle-fibre is of elongate fusiform shape, thickest in the middle, and pointed, more rarely forked, at the ends. The bulk of the fibre is composed of a highly contractile, doubly-refracting substance, which is not cytoplasm, but the product of the cytoplasm of the cell from which the fibre was formed.

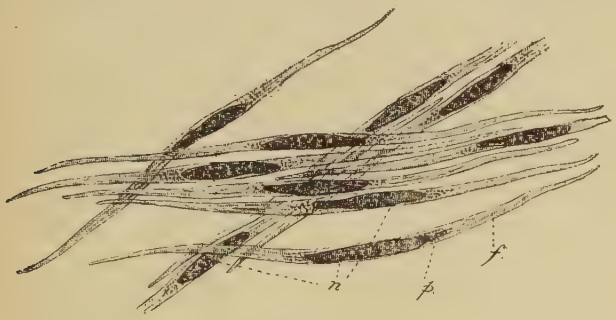

Fig. 17.

Group of unstriped muscle fibres from the bladder. *n*, the nuclei; *p*, the granular remains of the cell protoplasm; *f*, the longitudinally striated contractile portion.

The cellular character of each fibre is shown by the nucleus, which is generally elongated and oval, and exhibits an intra-nuclear network of chromatin. At each end of the nucleus are a few granules, the remains of the cytoplasm from which the contractile substance was formed. The plain fibres exhibit a faint longitudinal striation, and each is contained in a very delicate homogeneous sheath, which can only be seen when the fibre is twisted or torn across. The individual fibres fit closely side by side, and are gathered into larger or smaller bundles, which are attached to the connective tissue layers of the visceral organs.

Striped muscular fibre (fig. 18, *A*) from a skeletal muscle differs greatly in appearance from unstriped. The individual fibres are generally gathered together into bundles or fasciculi, and the bundles are united together to form the whole muscle. The last-named is invested by a sheath of connective tissue, called the **perimysium**, within which the bundles extend from end to end of the muscle, being only partially separated from one another by inward prolongations of the perimysium, the so-called **endomysium**. The bundles may be large or small,

according to the muscle from which they are taken, and each consists of a number of fibres varying from ·1 to ·01 mm. in diameter and 250 to 350 mm. in length in the human subject. Each muscle-fibre is invested by a transparent, homogeneous, elastic membrane, called the **sarcolemma**, which is particularly thick and strong in fishes and Amphibia. The individual fibres are not as long as the bundle which they compose, but end with tapering extremities, which cohere with neighbouring fibres, or at the ends of a muscle may be affixed to a tendon. Muscle fibres rarely branch, but an exception is found in the muscles of the frog's tongue, and also in the tongues and facial muscles of mammals.

The sarcolemma may be regarded as a tube whose contents are the muscular substance. This substance is of soft, semi-fluid consistency during life, but after death it becomes coagulated and firm. The most characteristic thing in the muscle-substance is its cross-striation. When viewed under the microscope each fibre exhibits a number of parallel cross stripes alternately light and dark. The fibre further exhibits a fine longitudinal striation, and certain methods enable us to break it up into a number of fine longitudinal strands, which run from end to end of the fibre, and are called **sarcostyles**. They are prismatic in section, and are separated from one another by a more fluid substance known as **sarcoplasm**, so that a transverse section of a fibre gives the appearance of a number of polygonal areas separated by lines representing the intervening sarcoplasm. Each isolated sarcostyle exhibits the same cross-striations as the whole muscle-fibre, and this appearance is due to the fact that the sarcostyle itself is made up of a number of segments, called **sarcomeres**, separated from one another by fine membranes, called the **membranes of Krause**, which in optical section appear as fine lines running across the middle of every bright band. An individual sarcomere consists of a median darker portion, which is called the **sarcous element**, and hyaline extremities abutting on the membranes of Krause. When the muscle-fibre is fully extended, the sarcous element divides into two portions, leaving a clear cross stria between them known as **the line of Hensen**. When the muscle-fibre is contracted the lines of Hensen become obliterated by the apposition of the halves of the sarcous elements, and the whole sarcomere being shortened,

the sarcous elements encroach upon the hyaline areas abutting on the membranes of Krause. At the same time each sarcomere becomes bulged out laterally, so that the whole sarcostyle has a moniliform appearance. It is held that the sarcous elements are composed of a denser protoplasmic substance, **spongioplasm**, and that the clear areas are occupied by a more fluid substance, the **hyaloplasm**, and that in the process of contraction the more fluid hyaloplasm is forced into or flows into the pores which permeate the spongioplasm of the sarcous elements. This, at least, is one explanation of the structure of striated muscular fibres, but it is held by other authors that a muscle-fibre is composed of a very regular intra-cellular network of modified highly contractile protoplasm, holding in its meshes a more fluid hyaloplasm, and that the optical effect of cross-striation is due to the regular arrangement of the network. It would be beyond the scope of this work to enter into a discussion of the relative merits of the rival theories, and it need only be remarked here that the theory of an intra-cellular network accords better with our present knowledge of the structure of protoplasm, than does the elaborate theory of sarcomeres, sarcous elements, etc., divided up by membranes. Both theories resemble one another in assuming the existence of a denser, actively-contractile spongioplasm, and a passive, more fluid hyaloplasm.

Cardiac muscular tissue (fig. 18, *B* and *C*) is, in some respects, intermediate between plain and striated muscular fibre. Its cellular components are not fused together, but remain distinct, so that the muscle appears to be made up of a number of oblong nucleated cells, joined end to end to form fibres, and communicating by short processes with the cells of adjacent fibres. Each cell exhibits cross-striations not unlike those of striated voluntary fibres, but less distinct.

Ordinary striped muscle-fibres are formed from somewhat elongated embryonic cells, which are at first simple and uni-nucleate. At the time of embryonic life when muscle is formed each cell elongates and its nucleus multiplies, so that a long multi-nucleate protoplasmic fibre is formed devoid of striae. The last-named first appear as longitudinal fibrils running along one side of the cell, and the whole has now the appearance of the very primitive epithelio-muscular cells found in some of the lower multi-cellular animals. At about this

time the sarcolemma is formed as a delicate membrane bounding the fibre. Presently cross as well as longitudinal striae make their appearance and invade the whole periphery of the fibre, the nuclei imbedded in a core of granular

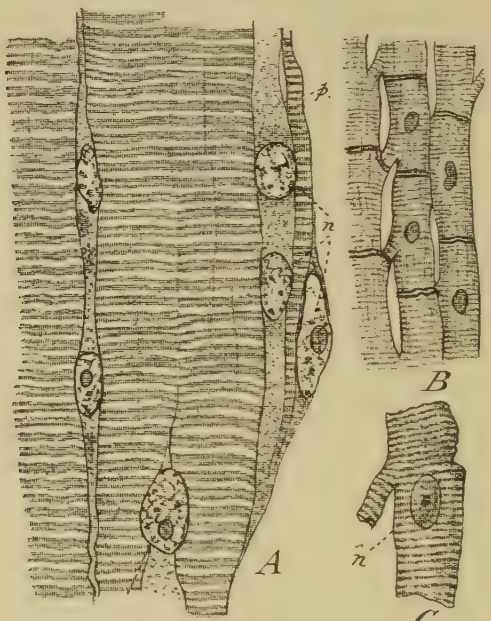

Fig. 18.

A, embryonic striped muscle-fibre from the tail of a tadpole, showing the nuclei *nn*, and the protoplasm *p*, of the cœnocyte from which the fibres are developed. The fibres exhibit alternate dark and light bands, and in the centre of each dark band is a light line, the line of Hensen; *B*, cardiac muscle-fibre showing the short branched nucleated cells; *C*, a single cell from cardiac muscle-fibre, more highly magnified, showing the cross-striation and the nucleus *n*. (*A* original; *B* and *C* from Schäfer.)

protoplasm occupying the centre. Eventually the striation and fibrillation extends to the centre, and the nuclei move outward to take up a superficial position under the sarcolemma. Thus it appears that, although the striated

muscle-fibre is often spoken of as a cell-fusion it is in reality not a product of many cells but of a cœnocyte.

The various organs and tissues which we have enumerated are supported by and attached to the skeleton, and are bound together and pervaded by **connective tissue**. The skeleton is composed of bone and cartilage, which are classified as varieties of connective tissue ; but we must regard the white membranous or fibrous material, which forms the sheaths of muscles and nerve-trunks, ties down the skin to the underlying tissues, and enters into the composition of tendons and aponeuroses, as constituting connective tissue proper, bone and cartilage standing somewhat apart from these.

Connective tissue may be studied to more advantage in mammals than in the frog. On cutting through the skin of a rabbit and stripping it from the body it is seen to be connected to the subjacent parts by a soft, white, tenacious, fleecy material known as **areolar tissue** (fig. 19). If a portion of this be carefully spread out as a film on a slide, and examined under the microscope, it is seen to be composed of a soft homogeneous ground substance or **matrix** in which are imbedded cells and bundles of extremely fine transparent **white fibres**, which traverse the matrix in all directions. These fibres do not branch, nor do those of one bundle cross over to and unite with those of another bundle, but keep a direction parallel with the remaining fibres of the bundle. They swell up in acetic acid, and are converted into gelatin on boiling. Each bundle usually pursues a wavy course, its component fibres maintaining their parallelism throughout the undulations. In addition, larger fibres may be distinguished which run nearly straight, or are thrown into large bold curves unlike the minute undulations of the white fibres. They differ also from the latter in the fact that they branch and anastomose with one another to form an open network, and also, when broken across, their ends tend to curl up. These are the **yellow elastic fibres** ; they are not affected by acetic acid, and do not yield gelatin on boiling, being composed of a different chemical substance called **elastin.**

The ground substance of areolar connective tissue stains, like intercellular substances in general, with silver nitrate, and it then exhibits a number of irregular cavities pervading a homogeneous basis. By staining connective tissue with other

dyes it may be shown that these spaces are occupied by branching cells, the so-called connective tissue corpuscles. There are three kinds of these cells, the **flattened** or **lamellar**, the **granular**, and the **vacuolated** or **plasma cells**. The first-named have a large oval nucleus and a finely granular protoplasm; their cell-bodies are produced into numerous branching processes, and the processes of adjacent cells may

Fig. 19.

Subcutaneous Areolar connective tissue from the rabbit, highly magnified, showing numerous wavy bundles of parallel white fibres, crossing one another in all directions; *el*, branched fibres of elastic tissue, some broken ends of which are curled up on the left of the figure; *bb*, branched connective tissue corpuscles; *g*, granular corpuscles; *f*, a fibrous corpuscle.

often be observed to unite with one another. They lie either imbedded in the matrix, where they occupy the spaces above referred to, or they may frequently lie on the surfaces of the bundles of white fibres, or between bundles which cross one another.

The granular cells are generally subspherical in shape, with an oval nucleus and a relatively small cell-body, in which are numerous coarse granules of a proteid nature. The granules stain deeply with certain acid dyes, such as eosin, and hence these cells are sometimes called **eosinophilcus**. The plasma cells are distinguished by the fact that their cytoplasm is filled with minute vacuoles, so that it has a bubbly or frothy appearance. That the corpuscles are concerned in the

nutrition of the connective tissue there can be no doubt, but the exact part played by each kind is not fully understood. They are often called fixed corpuscles, in opposition to intrusive leucocytes which are frequently found in the areolar tissue. But it seems probable, from the analogy of lower animals, that some, at least, of the connective tissue cells may have a migratory character.

Tendons and ligaments are a modified form of connective tissue, known as white fibrous tissue. In them the bundles of white fibres run in parallel courses instead of crossing one another irregularly, and are greatly preponderant over the elastic fibres. The corpuscles of fibrous tissue are all of the flat or lamellar variety, and tend to be disposed in rows or chains following the parallel arrangement of the bundles.

Some ligaments, such as the ligamentum nuchæ of the ox and other mammals, are composed almost entirely of yellow elastic tissue, and they are very elastic and extensible. Ordinary white tendons, on the other hand, are scarcely extensible.

It is clear that the bulk of a connective tissue consists of an intercellular substance which has been formed by the activity of the cells contained in it. In the course of development, connective tissue appears as an accumulation of amœboid undifferentiated cells, which presently send out ramifying processes which become united with one another to form a network. The meshes of the network are occupied by an albuminous fluid, which afterwards becomes changed to form the ground substance. The ground substance is at first homogeneous, but presently fibres are formed in it; how they are formed is not clear. Some think that they are the result of the actual conversion of cells into bundles of fibres; others think that the substance of the fibres is simply deposited in the matrix, the cells contributing the material without being themselves converted and used up in the process. The latter view is more probably correct, though there is little positive evidence on the subject.

The substance popularly known as gristle, but scientifically named **cartilage**, has many features in common with connective tissue. Like the latter, it consists of a homogeneous matrix in which cells are imbedded. If a thin slice of the white or pearly and translucent cartilage from the articular

head of a bone or from the hyoid, sternum, or supra-scapula of a frog be examined under the microscope, it is seen to consist of nucleated cells imbedded in a matrix of firm gelatinous consistency, which can easily be cut with a knife, but is at the same time highly elastic; it may be bent, twisted, or compressed, but readily recovers its size and shape when freed from the stress to which it was subjected. Like the intercellular substance of connective tissue, the matrix of cartilage is readily stained by nitrate of silver.

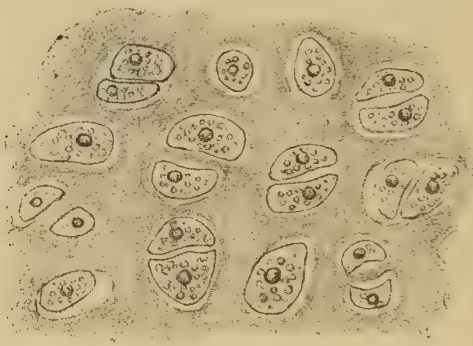

Fig. 20.

Part of a section through the xiphisternum of a frog to show the structure of hyaline cartilage. Several cartilage cells, many of them in groups of two, are imbedded in a hyaline matrix.

There are several kinds of cartilage, **hyaline**, **calcified**, and **fibrous cartilage**; the last-named may be yellow or white, according as the fibres in it are elastic or simply white fibres. We will concern ourselves chiefly with hyaline cartilage, so-called because of its homogeneous translucent matrix. The cells imbedded in it are rarely disposed singly and at equal distances from one another, but usually in groups or lines of two, four, or more, and it is often noticeable that in a group of two the cells are separated by a very small amount of intervening matrix, and that their adjacent sides are flattened as if by mutual pressure. Each cartilage cell is a subspherical or lenticular corpuscle of protoplasm, containing a rounded nucleus with a well-defined chromatin network, and a cell-body, in which fine granules and interlacing fibrils may often

be distinguished. The arrangement of the cells in groups is the expression of the fact that they multiply by division, and every group is made up of the daughter products of a single cell which originally occupied a central position within the group. The whole arrangement is best understood after a consideration of the development of cartilage. Primordial cartilage consists of an accumulation of polygonal cells (derived in the first instance from undifferentiated embryonic cells), each surrounded by a capsule (the product of the activity of the cell-protoplasm) of a transparent gelatinous-looking substance. The capsules of contiguous cells cohere together, and presently become fused, thus forming a scanty matrix. The cells meanwhile enlarge and undergo division, and at each division the daughter cells, lying in the single cavity of the parent cell, form each one a capsule for itself. The secondary capsules after a time cohere to and become blended with the matrix, and then each of the two daughter cells again divide, and each of the four cells of the second generation again forms a capsule for itself, which in its turn is blended with the matrix; and so on, as long as growth and active multiplication of the cells proceeds. But after a time the cells cease to multiply rapidly, and then each becomes surrounded by a number of concentric capsules which are successively blended with the matrix, and increase its mass. Thus it is evident that the matrix is a product of cartilage cells, and is probably secreted from their surfaces.

In many forms of cartilage the cells are, as described, rounded and isolated from one another in the matrix. It is difficult to understand how they are nourished, for the matrix is not vascular, nor can lymph channels be detected in it. In other forms, however, and especially in the cartilage of sharks and rays, the cells are not rounded but branched, and their prolongations ramify through minute canals in the matrix, and form a network of protoplasmic strands uniting the cells.

A great part of the supra-scapula of the frog consists of calcified cartilage. Here we find that granules of carbonate of lime have been deposited in the matrix in greater or less number. The lime can be removed by acids, when the structure of hyaline cartilage is made manifest, though it is somewhat altered by the presence of the cavities occupied by

the calcareous granules. Calcified cartilage is found in abundance in the skeletons of sharks and rays, and it must not be mistaken for bone, which is not present in these fishes; nor must any confusion be made between calcified cartilage and "cartilage bone," such as has been described as occurring in the skull of the frog. A cartilage bone is one which has taken the place of pre-existing cartilage, but has not been formed out of it. The replacement of cartilage by bone will be described after a consideration of the structure of bone itself.

Bone consists of an inorganic or earthy and an organic or animal part, intimately blended together. If a bone is steeped in dilute acid the earthy salts are dissolved out, and a model of the bone is left in a flexible, tough substance which is converted into gelatin on boiling. This last property is sufficient to distinguish the animal part of bone from cartilage, for the latter, after prolonged boiling, yields a substance of different chemical character called **chondrin**. The earthy parts of bone may be separated by burning out the animal part in a fire. They consist chiefly of phosphate of lime, with a small proportion of carbonate and a trace of fluoride of lime. Bone may be compact or spongy; in the latter case it is called **cancellous**. Cancellous bone, however, is made up of fine bars and partitions which have the same structure as compact bone.

If a thin slice of bone is viewed under the microscope it no longer appears dense and homogeneous, but is seen to be perforated by a number of holes, and a longitudinal section shows that these are the sections of a number of short longitudinal canals called **Haversian canals**. The calcareous substance is arranged round each Haversian canal in a series of concentric lamellæ. The concentric systems of adjacent Haversian canals nearly or quite touch one another, but are generally separated by vertical layers, which run parallel to the long axis of the bone and extend to its surface, where they form a peripheral layer. The arrangement of the lamellæ is made conspicuous by the presence of numerous little dark cavities, which are disposed conformably to the lamellæ in which they occur. These dark spaces are called the **lacunæ**. Each is connected centrally with the Haversian canal, peripherally with other lacunæ by numerous fine branching passages called the **canaliculi**. The Haversian

canals are occupied during life by blood-vessels—an arteriole and a venule to each—and a small amount of connective tissue containing branched cells. Some of the larger canals also contain marrow. Each of the lacunæ contains a small, nucleated, branched cell or **bone-corpuscle**, which com-

Fig. 21.

Portion of a transverse section through the femur of a pig to show the structure of bone. The section shows two concentric Haversian systems, each with its central Haversian canal, surrounded by numerous lacunæ with their canaliculi. At the top of the figure the external or periosteal layer is shown, in which the lacunæ are elongated in a direction parallel with the surface of the bone.

municates by means of protoplasmic processes running through the canaliculi with the processes of adjacent corpuscles, and eventually with the branched connective tissue cells of the Haversian canal. The outermost canaliculi of a Haversian system do not, as a rule, communicate with those of an adjoining system, but bend round to join the peripheral lacunæ of their own system. The elaborate system of blood-vessels and nucleated cells with communicating protoplasmic processes shows that the nutrition of bone is dependent on the presence of living protoplasm, and the whole structure of bone may be compared to that of connective tissue, the gelatin plus lime salts forming the matrix, the bone-

corpuscles being homologous with ordinary connective tissue-cells. In fact, true bone is formed in connective tissue, whether it be what we call "cartilage bone," or whether it be "membrane bone." It must be borne in mind that when we speak of a "cartilage bone," such as the ex-occipital or pro-otic of a frog's skull, we do not mean that the cartilages of the cranium or of the otic capsule have been transformed into bone. We only mean that the bone has been preceded by cartilage, which latter has been absorbed and replaced by bone in the manner to be described. There must be no confusion between calcified cartilage and true bone. Cartilage is a non-vascular tissue; bone, with its system of blood-vessels running in the Haversian canals, is highly vascular. Bone, as has been said, may be developed directly from membrane, without being preceded by cartilage. To take, as an example, the parietal bone of a mammal, such as a sheep. Between the **dura mater**, as the connective tissue layer surrounding the brain is called, and the outer integument, is a layer of connective tissue, composed of a matrix with fibres and numerous granular corpuscles. It is in this membrane that each parietal bone appears in the form of a number of spicules of bone radiating outwards from a "centre of ossification," and joined together at intervals by short, irregularly-placed tangential bars. The outer end of each radial spicule is prolonged for some distance beyond the actual calcareous spicule in the form of a bundle of parallel or slightly divergent transparent fibres, the so-called **osteogenic fibres**. They resemble white connective tissue fibres, except that they are straighter, stiffer, and are less distinctly fibrillated. The osteogenic fibres are covered by a layer of granular cells called **osteoblasts**, applied to the surfaces of the fibres and occupying their interstices when they diverge from one another. The osteoblasts appear to form the osteogenic fibres, and also to supply the calcareous deposit which is laid down in the form of minute granules in the matrix between the fibres. Eventually, by their coalescence, the granules form the substance of the bone, the latter first appearing as a network of spicules and splinters, but as ossification proceeds the spaces between are gradually filled up by the continued deposition of calcareous granules. In many cases, however, the interstices are occupied by blood-vessels, and these are surrounded by the advancing bone, and eventually form the

canals of the Haversian systems. Some of the osteoblasts become imbedded in the advancing bone, and remain as the bone-corpuscles of the future lacunæ.

The so-called ossification in cartilage can be very well studied in a long bone such as the tibia or femur. In the first place, a small model of the future bone is laid down in cartilage, and this is surrounded by a vascular membrane which will become the future covering or **periosteum** of the bone. When ossification is about to commence the cartilage-cells in the middle of the model become much larger and flatter, and are arranged in a number of rows or columns parallel to the long axis of the bone. The matrix between them becomes calcified by deposition of calcareous granules. In the meantime true bone is being formed outside the cartilage, between it and the periosteum. The last-named membrane is vascular, and contains numerous granular cells, chiefly on its inner surface nearest to the cartilage. From these **osteoblasts**, osteogenic fibres are formed, and true bone containing blood-vessels and bone-corpuscles is formed just as in the case of membrane bone. At this stage the developing bone consists of a core of calcified cartilage enclosed in its middle portion by a sheath of membrane bone. Presently the vascular and osteoblastic tissues break through the sheath of newly-formed bone and burrow their way into the cartilage, which is for the most part absorbed by the agency of certain giant-cells containing several nuclei, and known as **osteoclasts**. A network of bony spicules is developed from the intrusive osteoblasts in the cavities formed by the absorption of the cartilage, and this network carries blood-vessels in its meshes just as is the case in membrane bone. Gradually the whole of the cartilage of the shaft is absorbed and replaced by a spongework of bone, which for a long time remains spongy or "cancellous," but eventually is solidified in the peripheral parts of the shaft by the deposition of concentric layers round the blood-vessels, whilst the central portion is absorbed, and a central cavity, the medullary space, is left in the middle of the bone.

Before leaving the subject of connective tissue, mention may be made of fat-cells, which, although their function is essentially metabolic, are nothing more in their origin than connective tissue corpuscles in which droplets of fatty matter

have been formed by the activity of the cell-protoplasm. Fatty or **adipose tissue** appears under the microscope as a number of minute oval vesicles, generally gathered into a cluster called a lobule, which receives an afferent artery and an efferent vein. Each vesicle is filled with an oily matter which can be dissolved out by the action of ether, and it can then be seen that the vesicle consists of a very delicate structureless membrane, on one side of which is a flattened nucleus, surrounded by a few granules of protoplasm. In some

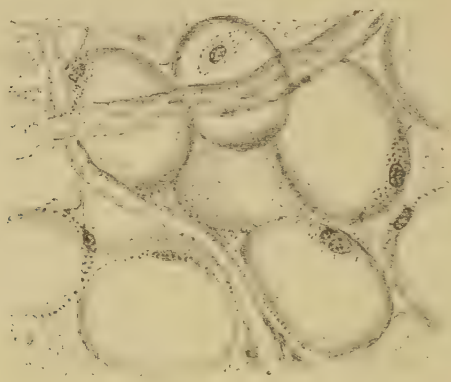

Fig. 22.

Part of a fat lobule from the mesentery of a rabbit, highly magnified, to show the structure of adipose tissue. (From a drawing by Dr E. H. Schuster.)

of the vesicles a wide-meshed reticulum of delicate protoplasmic strands may be seen, in the cavities of which the oil-drops were lodged. A fat-cell is a good example of the endoplastic formation of material by a living cell.

We have now studied the microscopical characters of the tissues sufficiently to enable us to comprehend the fact that the whole organism is composed of a number of minute living units called cells, which, indeed, are seldom to be found in a primitive and undifferentiated condition in the adult animal, but are variously modified, changed, and adapted to particular purposes, and consequently exhibit every variety of form and

every sort of relation to one another. It is true that there are some tissues, such as cartilage and bone, the bulk of which is not formed of cellular elements but of a non-cellular, more or less homogeneous matrix. It is evident, however, that this matrix has been formed by the activity of the cells which remain enclosed within it ; and these tissues do not contradict the general statement that the body of the frog, as indeed of all animals, is composed of cells. It is of the utmost importance that the part played by cells in the formation of animal and vegetable tissues should be clearly apprehended by the student. It has been seen that most of the cells are specialised, or, as it is generally said, are **differentiated.** This means that the cell-protoplasm has been active in various ways, and has given rise to substances which are either stored up within the body of the cell (as, for example, the fat-cell), when they are said to be **endoplastic products,** or are formed on the outside of the cell as a sort of envelope (as in the case of cartilage or bone-cells), in which case they are called **ecto-plastic products.** And in all cases we see that differentiation means the exaltation of one of the fundamental properties or functions of living matter at the expense of the others. Thus nerve-cells are essentially irritable, this fundamental property of protoplasm being exalted, whilst others, such as contractility, metabolism, etc., are depressed. Gland-cells are essentially metabolic and secretory, muscle-cells are essentially contractile ; and so forth. In every case, also, the exaltation of a special function or attribute of the protoplasm is accompanied by a change of form, a morphological differentiation. The nerve-cell differs from the muscle-cell, and both differ from the gland-cell in their obvious structural qualities. Further, we can see that amongst the countless cells of which such an organism as the frog is composed, large groups of cells have become specialised for the performance of special functions, some undertaking one special kind of work, some another kind ; yet they are not independent units acting for themselves without regard to the other kinds with which they are associated, but, contrariwise, they act and interact harmoniously, as it seems purposefully, for the benefit of the organism as a whole. The multi-cellular animal has often been described as a cell-colony, in which there are cell-castes, the members of which undertake special kinds of labour; and so it has

become common to speak of a physiological division of labour amongst the cell-castes, with a corresponding morphological differentiation of form. The illustration is a useful one, but it ceases to be valuable if pushed too far. The cells composing the frog's body are not independent units in the sense that the individual men composing a colony are individual units. Their life not only contributes to the life of the whole, but is indissolubly connected with it; and in this connection it should be borne in mind that, however much the other functions of an individual cell may be depressed in order that its special function may be exalted, all cells retain and must retain one vital attribute, that of assimilation. All cells, whilst they retain their vitality, must be nourished, and they are nourished by the blood through the intermediary of the lymph. Each cell has its own kind of metabolism; but the metabolism of each, whilst it contributes to the whole, is merged into the metabolism of the whole, and ceases when it is removed from it, except in one case, to be considered directly.

All these considerations and facts are collected together in what is known as the **Cell-Theory**, which was first propounded, for the vegetable kingdom, by Schleiden, a botanist, in 1838. Schleiden's views were adopted and applied to the animal kingdom by Theodore Schwann in 1838 and 1839.

The continuous researches of botanists and zoologists have added much to the cell-theory since the days of Schwann, and at the same time have rendered his position less tenable. Schwann made a fundamental error regarding the genesis of cells. He supposed that they were formed, in a manner analogous to crystallisation, out of a nutrient matrix, which he called the cytoblastema. He supposed that the cell was a hollow vesicle containing another vesicle, the nucleus, and that this again surrounded a smaller vesicle, the nucleolus. The nucleolus, according to his views, was first deposited in the structureless or minutely granulous cytoblastema, and it formed a centre of attraction round which other molecules were deposited to form the nucleus. This, again, continued to attract fresh molecules, which formed the cell-body.

The error of this view was pointed out in 1851 by Robert Remak, who showed that all the cells of which an animal body is composed are formed by the continuous and repeated sub-

division of an originally single and simple cell, the ovum or egg-cell, and that there is no evidence of cells being formed autogenously, like crystals out of their mother liquor, as Schwann had supposed. The continued labours of many investigators have confirmed Remak's conclusions, and it is now an established fact, universally assented to, that every cell arises from the division of a pre-existing cell, a generalisation neatly summed up in Virchow's aphorism, *Omnis cellula e cellulâ*.

It was observed at a comparatively early date that the nucleus took an important if not a predominant share in the reproduction of cells by division, but the significance of this fact was for a long time obscure, and did not attract much attention until the discovery by Anton Schneider in 1873 of remarkable form-changes undergone by the nuclei of dividing tissue-cells. Schneider's observations were followed up by a host of observers, amongst whom the names of Fleming, Fol, Ed. van Beneden, and Hertwig must always occupy an honourable position; and it has been demonstrated that the phenomena first observed by Schneider are of normal occurrence, not only in dividing tissue-cells, but also in the germ-cells, the developing ova and spermatozoa of multi-cellular animals, and in a large number of simple uni-cellular animals, or Protozoa.

The phenomena are generally known as **karyo-kinesis**, but the word **mitosis** is also used to denote them, and it is, on the whole, the more convenient term, though it must yield priority to the other.

As has already been said, division of the cell-body is always accompanied by and generally preceded by division of the nucleus. In certain, but comparatively rare, cases the nucleus divides quite simply. It becomes elongated, and then dumb-bell shaped. The strand connecting its swollen ends becomes thinner, and finally breaks, so that two new nuclei are formed. The cell-body becomes constricted in its middle and eventually is separated into two halves, each containing a portion of the divided nucleus. Such a mode of nuclear division is known as simple or **amitotic**. It occurs in some Protozoa, in some leucocytes, and characteristically in certain cells forming morbid growths. But in the great majority of cases the process is of a far more complex kind, and it differs somewhat

in tissue-cells and in germ-cells. We will take the former case first, as being the simpler.

A resting nucleus has the characters depicted in figure 23, *A*. Its nuclear membrane is evident; and within the membrane the deeply-staining chromatin is distributed in the form of granules over an achromatic reticulum or network, which often exhibits thickenings or nodes at the points where the linin threads are, as it were, knotted together to form the network. These thickenings are not to be confounded with the nucleolus, whose share in the process of mitosis is somewhat obscure.

Outside of the nuclear membrane, lying close to it in the cytoplasm, is a very minute but very important body, known as the **centrosome**. It is often surrounded by a little specialised mass of cytoplasm, known as the **centrosphere**. The division of the cell appears to be heralded by changes in the centrosome and the cytoplasm immediately surrounding it. The centrosome divides into two parts, which travel round the periphery of the nucleus to take up positions at opposite poles. As it divides and travels round, each moiety of the centrosome becomes surrounded by a number of radiating fibrillæ stretching into the adjoining protoplasm, and so forming a characteristic star-shaped figure to which the name of the **astral figure** has been given, the fibrillæ being known as the **astral rays.**

Meanwhile important changes have been going on in the nucleus. The linin network breaks up and resolves itself into a convoluted thread known as the **skein** or **spireme**. The chromatin increases in quantity, possibly at the expense of the nucleolus, stains more intensely than before, and is distributed in the form of granules or minute discs along the linin thread. In a short time the spireme breaks up into a number of segments of equal length, which may be straight and rod-shaped, or curved into a horseshoe shape, or may be simply spherical or ovoid masses. In some cases the curved rods may be joined together by their ends to form rings. But their shape is relatively unimportant, the essential thing is that the spireme is resolved into a definite number of equal masses, called **chromosomes**, and it has been asserted that every species of plant or animal has a fixed number of chromosomes, which number recurs in every division of every

tissue-cell in the body. The number may be very large—it is said to be one hundred and sixty-eight in a certain crustacean

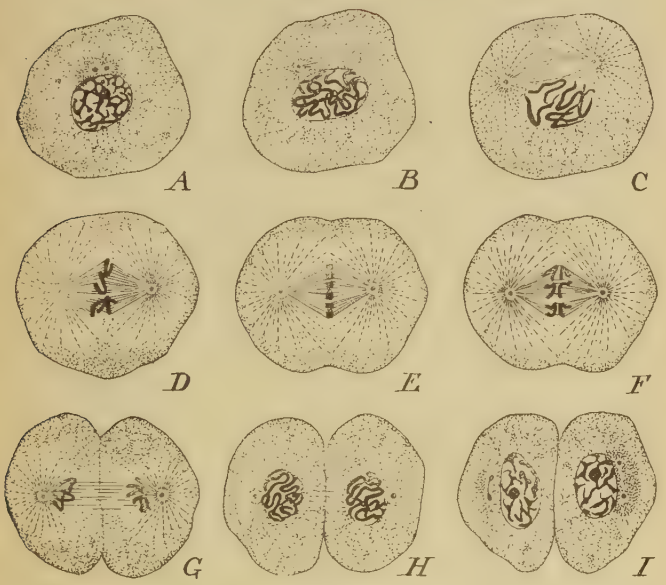

Fig. 23.

Diagrams representing the essential phenomena of mitosis. *A*, a cell with resting nucleus containing a chromatic reticulum and a single nucleolus. The centrosome is double and surrounded by the centrosphere. *B*, the centrosomes are separating and each is surrounded by astral rays; the chromatin forms a convoluted thread or spireme. *C*, The spireme is broken up into a number of V-shaped chromosomes, the polar spindle is formed between the now widely separate centrosomes. *D*, The chromosomes attached to the spindle-fibres are arranged at the equator of the spindle. *E*, division of the chromosomes, which are viewed end on. *F*, divergence of the chromosomes. *G*, chromosomes collecting at the poles of the spindle, the space between them occupied by interzonal fibres; commencement of division of the cell-body. *H*, *I*, complete division of the cell, and reconstitution of the nuclei. In *I* the centrosomes are dividing preparatory to a new mitosis. Note *A*-*D* = prophase; *E* = metaphase; *F*, *G* = anaphase. *H*, *I* = telophase.

known as *Artemia salina*,—or it may be very small, as in the thread-worm parasitic in the intestines of the horse (*Ascaris megalocephala*). Recent researches, however, render it doubt-

ful whether the number of chromosomes in tissue-cells is as constant as was at one time supposed.*

At the time when the chromosomes are formed, the nuclear membrane has generally been absorbed, and has disappeared, leaving the chromosomes apparently free in the cytoplasm, and at the same time an important and remarkable structure makes its appearance in the position formerly occupied by the now broken-up nucleus. This is the **spindle**, composed of a number of fibrillar threads converging at each end of the spindle towards the centrosomata, and diverging from one another in the centre, or, as we may call it, the equator of the spindle. There is some doubt as to whether the spindle is formed out of the substance of the cytoplasm or out of the achromatic substance of the nucleus. In a large number of cases, at all events, the spindle fibres appear to be formed in two groups which have different origins: an internal group, forming the axis of the spindle, is formed from the linin threads of the nucleus, and an external group, forming the periphery of the spindle, is derived from the cytoplasm, and probably from that modified part of it which has been described as the attraction sphere or centrosphere. It should be noticed that in some cases—*e.g.* the tissue-cells of the salamander—the spindle at its first origin lies wholly outside the nucleus, and is formed entirely under the influence of the centrosomata.

The spindle and the two asters surrounding the centrosomata do not stain easily with the ordinary dyes, and hence are often called the **achromatic figure**, or **amphiaster**, but the centrosomata themselves stain readily and intensely with certain dyes.

However the spindle may be formed, its eventual relation to the chromosomata is the same. The latter become attached to the spindle fibres in such a manner as to form an equatorial ring round the spindle. The whole of the stages which have been described constitute what is known as the **prophase** of mitosis, and may be regarded as preparatory to the next and most essential step, the **metaphase**. This consists in the division of the chromosomata into equal halves. (Fig. 23, *E*.) If they are rod-shaped or horseshoe-shaped the chromosomata split into two lengthwise, if round or ovoid they simply divide

* J. B. Farmer and D. Shove, On the structure and development of the somatic and heterotype chromosomes of Tradescantia virginica.—*Quart. Journal of Microscopical Science*, xlviii. (1905) p. 562.

into two, and each half so formed travels in opposite directions along the spindle-threads towards the poles of the spindle. The metaphase now passes into the final stages of the process known as the **anaphase.** The divergent groups of chromosomata become closely crowded into a mass at each pole of the spindle in the centre of the astral rays, and the space previously occupied by the spindle is traversed by a bundle of fibres, known as the connecting or **interzonal fibres.** In plant cells, and in some animal cells (*e.g.* in cartilage) the interzonal fibres are thickened in the equatorial region of the spindle to form the so-called equatorial plate. The last stages of mitosis are known as the **telophase.** The groups of chromosomata at each pole of the spindle are reconstituted into a new daughter-nucleus, usually going through the processes of the prophase in a reversed direction. Thus the chromosomata become united to form a spireme, and the spireme breaks up into a reticulum, the nuclear membrane re-appearing in the spireme stage. Whilst this is going on, the cell-body is divided into two in a plane passing through the equator of the spindle. In plant cells, and some animal cells in which an equatorial plate is formed, the division is effected by the formation of a septum across the cell-body in the plane of the equatorial plate. But in most animal cells division of the cell-body is effected by a simple constriction which gradually deepens and divides the cell into two. The asters generally disappear, or are reduced to a spherical mass surrounding the centrosome, constituting a centrosphere. The results of this truly remarkable process are obvious. The nucleus of each daughter-cell receives exactly half the chromatin of the nucleus of the mother-cell. Nor is this all; one half of each individual chromosome passes to one, the other half to the other daughter-nucleus. When division of the cell is complete a resting stage follows, during which the nucleus of each daughter-cell grows to the size of the original mother-nucleus, the chromatin sharing in the growth of the whole nucleus; and when the normal size is attained the prophase is again entered into, and a fresh mitosis with a new division of the cell takes place. The behaviour of the centrosome demands some attention. This minute body seems to lead the way in cell-division. The two halves into which it divides form the centres of the asters and the poles of the

spindle; they determine, by the positions which they take up, the direction of the spindle, and consequently the plane in which the cell-division will take place. It is evident that this plane must always be at right angles to the long axis of the spindle. The centrosomata sometimes divide very precociously during the telophase or even during the anaphase of mitosis, and the two products then remain in each daughter-cell throughout the resting stage. On the other hand, there are cases in which the division of the centrosome is retarded until after the formation and even after the segmentation of the spireme. It is clear, therefore, that the centrosome and the chromosomes act independently of one another in the process of cell-division.

The details of mitosis differ in different animals and plants, but the end result in tissue-cells is always the same, the chromatin of the mother-nucleus is divided into two equal and like halves which are distributed to the daughter-nuclei. The only real exceptions occur in abnormal and pathological cases, such as cancer-cells, which need not detain us here. But, whilst the equal division of the chromatin is the rule for tissue-cells, the case is different for germ-cells.

The generative organs of the frog are recognisable at a very early period in its life history. In a tadpole of about 10 mm. length an accumulation of primitive germ-cells may be seen lying between the two folds of the peritoneal epithelium forming the origin of the mesentery in the middle third of the pleuro-peritoneal cavity. In a microscopical preparation the cytoplasm of the primitive germ-cells is seen to be filled with platelets of reserve material or yolk, the presence of which makes these cells easily distinguishable from the neighbouring epithelial and connective tissues. The rudiment of the generative organs is at first unpaired, but it soon becomes a flat band and is divided lengthwise into right and left halves which, as growth proceeds, project into the pleuro-peritoneal cavity as two ridges lying right and left of the mesentery, and covered in below by the flattened peritoneal epithelium. The primitive germ-cells increase in size, seemingly at the expense of the reserve material stored up within them, for by the time that they have attained their full size the yolk platelets have disappeared. The primitive germ-cells then multiply by a number of successive divisions, in which the nuclear mitoses are

similar to those observed in dividing tissue-cells. For reasons that will presently become apparent these nuclear divisions are described as **pre-meiotic.*** The products of division of each primitive germ-cell remain close together, so that a number of cell-clusters are formed, separated from one another by ingrowths of the adjacent connective-tissue. Up to this period there is no distinction of sex, but about the time of the metamorphosis of the tadpole into the frog, further changes take place leading to the formation of ova in the female or spermatozoa in the male.

In the female frog each cell-cluster is transformed into an **oocyte** (more rarely two or more oocytes) surrounded by a sac or follicle formed by the remaining cells of the cluster. This process, however, does not take place simultaneously in all the clusters: only a few develop at one time, the others remain in a dormant condition, and form a provision for successive crops of oocytes in recurrent breeding seasons. The follicular cells elaborate reserve material from the blood and lymph and pass it on to the oocytes, where it is stored up in the form of granules of **deutoplasm** or food-yolk. As a result of this storage of reserve material, the oocyte increases greatly in size, and at the same time its nucleus becomes larger and the nuclear membrane and chromatic reticulum more distinct. When it has attained a diameter of about ·5 mm., a thin structureless envelope, the vitelline membrane, is found around it, and rather later black pigment is deposited, at first over the whole surface, but afterwards it is restricted to one hemisphere. By continued deposition of yolk in their cell-bodies the oocytes grow till they attain the size of small shot, and project in bunches from the surface of the ovary. They then go through a process known as maturation, during which each divides twice into two very unequal portions. At each division the nucleus undergoes mitosis. The first mitosis differs to a considerable degree from the normal: it was formerly described as the **heterotype**, but more recently has been called the **meiotic** division. The second division is normal: formerly known as the **homœotype** it is now called

* I take the liberty to alter the spelling adopted by the authors of the name. It is derived, they tell us, from μειωτικόν, a thing divided, and, this being so, the English rendering should surely be "meiotic," not "maiotic."

the **first post-meiotic** division. The two small cells formed by the successive divisions of the oocyte are known as **polar bodies.** While the maturation is in process the ova are discharged into the body-cavity by the bursting of their follicles; they are passed along partly by muscular contractions of the abdominal walls, partly by ciliary action, to the mouths of the oviducts, and travel down the oviducts into the uteri. During its passage down the oviducts each ovum is invested by a coat of slime or mucin secreted by the glands with which the oviducal walls are abundantly supplied. The ova accumulate in great numbers in the highly distensible uteri, and eventually are expelled through the cloaca into the water, in which the mucin investment swells up to form the well-known jelly of frog's spawn.

At the time of their passage to the exterior the ova are fertilised by the simultaneous discharge of the semen of the male frog. Without fertilisation they are incapable of further development; but if fertilisation takes place each ovum goes through a series of divisions which result in the formation of a multi-cellular aggregate, leading up to the tadpole and culminating in the adult frog.

The spermatozoa of the male are derived from the cell-clusters described above. At first the cells of each cluster are all alike, but as development proceeds those more centrally situated become **spermatogonia** and those more peripherally situated form a sac or follicle investing them. The spermatogonia divide and subdivide, with normal pre-meiotic nuclear mitoses, till, after a time, they come to rest and increase in size. They are now known as **spermatocytes.** Each spermatocyte divides equally into two, and each of these again divides into two, making four **spermatids** derived from each spermatocyte. In the first division the nuclear mitosis is of the heterotype or meiotic kind: in the second division it is of the homœotype or first post-meiotic kind. Each spermatid is directly changed into a spermatozoon. The spermatozoon of the frog consists of (1) a head, which differs somewhat in shape in different species of frogs; (2) a minute segment immediately behind the head, which appears to consist of cytoplasm with a contained centrosome; (3) a whiplash-like tail or flagellum by whose movements the spermatozoon is propelled through liquid. The head consists entirely of nuclear matter, except for a very thin layer of cytoplasm which forms an investment to it.

The heterotypic or meiotic nuclear mitoses which accompany the first division of the spermatocyte, and the division of the ovum forming the first polar body, are of great interest because they result in the reduction of the chromosomes to half the normal number. Though their main features are fairly well known in the frog, the whole process has not been so thoroughly

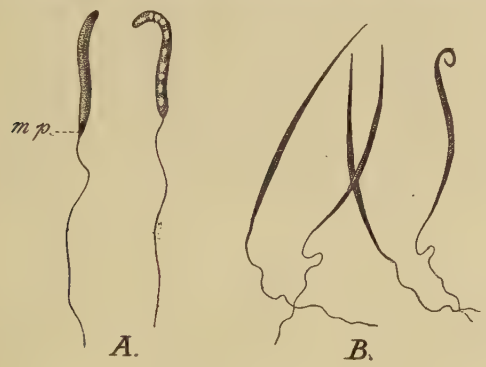

Fig. 24.

A, Spermatozoa of *Rana esculenta*. *B*, Spermatozoa of *Rana fusca* (after Leydig). *mp*, middle piece.

worked out in this as it has been in some other animals, and the following account, while applicable to the frog, must be understood to be a general description of the nuclear changes as observed in animals and plants. To begin with the spermatozoon. The spermatogonia, throughout their repeated divisions, exhibit the same number of chromosomes as the tissue-cells of the body, this number in the frog being twenty-four. In the first or meiotic division of the spermatocyte this number is obscured, and the behaviour of the nucleus is from the first somewhat different from that observed in ordinary cell divisions. Some of the details of the process are shown in fig. 25, *A-F*. The nucleus is situated excentrically in the cell-body so that one side of the latter appears to be richer in protoplasm than the other. On this side, overlying the nucleus like a cap, is the denser and more granular centrosphere containing the centrosomes. The nucleus about to enter upon the meiotic division is more than usually chromatic. Much of the chromatin is distributed in the form of scattered granules

along the achromatic network, but much of it is concentrated in the karyosome, where it forms a rind or investment to a central corpuscle of achromatic plastin. The ribbon-like spireme that emerges from the network exhibits a distinct polarity, the loops of the ribbon being gathered up towards the pole of the nucleus nearest to the centrosphere. The karyosome occupies a more or less central position, with the loops converging towards it. The spireme ribbon is at first slender and the chromatin is evenly spaced along it in the form of a single row of bead-like granules (fig. 25, *B*). After a while the loops spread out again, the ribbon becomes thicker, and there is an obvious increase of chromatic material. It is probable that this increase is due in part at least to the continual transference of chromatin from the karyosome to the spireme. At all events the karyosome gradually loses its chromatic investment and disintegrates, its remnants being eventually cast out into the cytoplasm. As the ribbon thickens it is split longitudinally throughout its entire length. Each chromatin bead first divides into two and afterwards the achromatic substance is divided, the spireme at this stage appearing as a double row of deeply stained beads supported by two parallel ribbons of achromatic material (fig. 25, *C*). At the same time the loops become more distinctly separated from one another and contract towards the centrosphere. As contraction proceeds, the longitudinally split ribbon is divided transversely into twelve U-shaped loops whose open ends are directed towards the centrosphere. Close inspection shows that each loop is formed of two bent segments united end to end at the bend of the U, and this observation is confirmed by the study of the subsequent history of the loops. Thus, though there are apparently twelve U-shaped chromosomes — that is to say, half the number typical of the pre-meiotic divisions — there are in reality twenty-four, each loop being a double or, as it is called, a **bivalent** chromosome, formed by the union of two chromosomes end to end. The process which results in the emergence of the chromosomes in pairs is known as **synapsis.** The longitudinal split observed in the previous stage is also recognisable in each bivalent chromosome, and in the accompanying figures it is represented as persisting through the metaphase and anaphase, though it usually disappears to reappear again at a later period. It should be clearly understood that

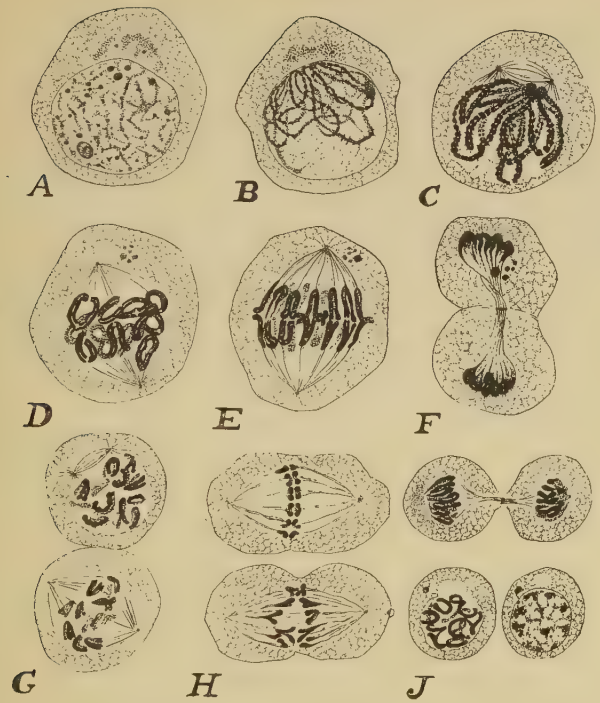

Fig. 25.

A, A spermatocyte preparing for the first or meiotic division; a large karyosome is present and the rest of the chromatin is scattered in the form of granules on the achromatic network of the nucleus; on the top of the nucleus is the centrosphere with two centrosomes. *B*, spireme with a single row of chromatin granules; the loops of the spireme show a distinct polarity. *C*, early stage of synapsis, the chromatin granules and the spireme ribbon are divided longitudinally. *D*, twelve *bivalent* chromosomes of various shape becoming arranged round the equator of the spindle. *E*, metaphase of the meiotic division; each bivalent chromosome is being divided into its two components, one of which is being drawn to each pole of the spindle. *F*, nuclear telophase and first division of the spermatocyte. *G*, two secondary spermatocytes preparing for division; the upper figure showing an earlier stage of mitosis than the lower; the nucleus of each spermatocyte contains twelve *univalent* longitudinally-split chromosomes. *H*, the upper spermatocyte shows the metaphase, the lower the early anaphase of the first post-meiotic (homœotype) division. *J*, the two secondary spermatocytes have divided to form four spermatids; the nuclei are shown in different stages passing from the late anaphase to the resting condition. Note that the figures *G*, *H*, *J* are drawn on a somewhat smaller scale than the rest.

the longitudinal split has nothing to do with the bivalent character of the U-shaped chromosomes.

By this time the karyosome has broken up into fragments which are cast out into the cytoplasm. The nuclear membrane disappears, the centrosomes diverge from one another and spindle-fibres are formed between them. As the external spindle-fibres are formed the bivalent chromosomes appear to be caught up by them and carried to the equator of the spindle. In this position their bivalent character is often obvious, but their actual shape is variable. They may have the form of horseshoes, rings, figures-of-eight, or crosses, but in each case can be seen to be made up of two parts. A horseshoe is two longitudinally split curved rods joined together by one end; a ring is composed of two similar rods joined together by both ends: a figure-of-eight is a twisted ring, and so forth. When the spindle is fully formed the bivalent chromosomes are arranged around its equator in such a way that one component of each is directed towards one pole, the other component towards the other pole. In the metaphase the two components are simply drawn apart, so that the two daughter-spermatocytes have each twelve **univalent** chromosomes, the number having been reduced by the division of each bivalent chromosome into two. This mode of division is therefore very appropriately called a meiotic or reducing division. As soon as it is completed the two daughter-spermatocytes, each containing twelve univalent longitudinally split chromosomes, prepare for a new division. Two stages of the prophase are shown in fig. 25, *G*. The longitudinal split, even if it has been obscured or has altogether disappeared in the preceding changes, again becomes very apparent in each of the twelve chromosomes. The last-named are arranged round the spindle in such a manner that the longitudinal split in each coincides with the equator, therefore with the half of a chromosome on either side of it. In the metaphase these halves are pulled apart (fig. 25, *H*); the anaphase and telophase follow in the usual manner, and the whole process results in the formation of four spermatids, each containing half the normal number of chromosomes. The spermatid is directly converted into a spermatozoon by a series of changes of form and growth too complicated to be described here. The process of the maturation of the ovum

is essentially the same as that described for the spermatozoon, the difference being that, whereas the two successive divisions of the spermatocyte result in the formation of four spermatids, each of which becomes a spermatozoon, the two successive divisions of the oocyte result in the formation of four cells, three of which are minute polar bodies and are to be regarded as abortive ova, while the fourth is of large size, is filled with deutoplasm, and is the definitive ovum, ready for fertilisation. The nuclear changes, however, are identical in character. The first division of the oocyte is the meiotic or heterotype division, resulting in the distribution of one of the components of each of the twelve bivalent chromosomes to each of the cells formed by the division. There are therefore twelve univalent chromosomes in the first polar body and twelve in the oocyte. The second division of the oocyte is homœotypic, and each of the twelve chromosomes is divided longitudinally, one product of division passing into the second polar body, the other remaining in the ovum. The first polar body does not always divide again; if it does the division is homœotypic, and resembles the second division of a spermatocyte. In all four cells then, the ovum and the three polar bodies, there are twelve univalent chromosomes, just as there are in the four spermatids. But the polar bodies are not destined for further development: they may persist for some time under the vitelline membrane but eventually disintegrate and disappear. The ovum is likewise incapable of further division and development unless it is stimulated thereto by fertilisation.

Two distinct processes are involved in the act of fertilisation. Firstly, the union of the sperm-nucleus with the egg-nucleus, whereby the full number of chromosomes characteristic of the species is restored. This process is believed to be intimately connected with the transmission of the heritable qualities of both parents to the offspring. Secondly a stimulus is conveyed to the ovum by the spermatozoon, under the influence of which the latter divides and gives rise to a new multicellular organism.

Briefly told the phenomena of the fertilisation of the amphibian ovum are as follows:—The spermatozoon, including head, middle piece and tail, enters the ovum at any point of the pigmented hemisphere and at the point of entry a deep funnel-shaped pit is formed, at the bottom of which lies the

spermatozoon. The mouth of the funnel is then filled by a plug of coagulated material known as the **entrance-cone.** A

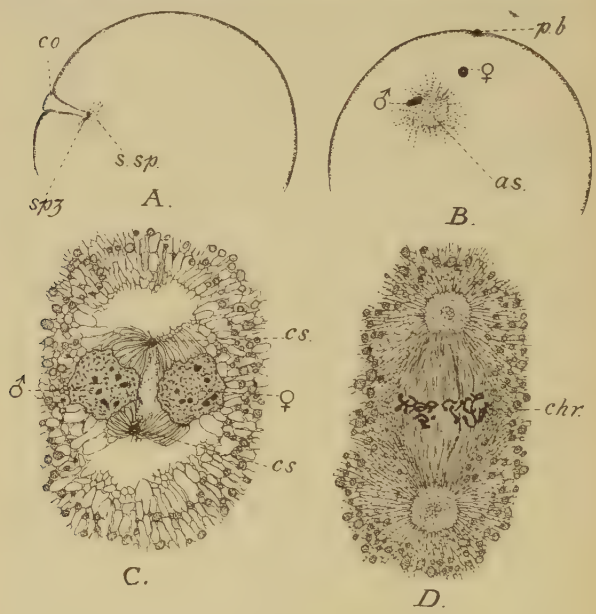

Fig. 26.

Fertilisation of the amphibian ovum (after Jenkinson).

A, outline drawing of a section parallel to the axis of the egg; the superficial pigment of the animal hemisphere of the egg is indicated, but the yolk granules are omitted. *co*, entrance cone; *spz*, spermatozoon lying at the bottom of the entrance funnel; *s.sp*, spermsphere. *B*, a meridional section through the egg at a later stage; ♂, sperm-nucleus, also called the male pro-nucleus; ♀, egg-nucleus, also called the female pro-nucleus; *as*, sperm-aster; *pb*, polar body. The size of the sperm- and egg-nuclei has been exaggerated. *C*, portion of a section through an egg showing an early stage in the formation of the fertilisation spindle, highly magnified; ♂, sperm-nucleus; ♀, egg-nucleus; *cs*, centrosomes. *D*, portion of a section of an egg showing the early stage of the metaphase of the fertilisation spindle; *chr*, the chromosomes derived from the sperm- and egg-nuclei lying unevenly, but still in two distinct groups, in the equatorial plane.

clear space is formed round the head and middle piece of the spermatozoon, the tail is absorbed, and soon the middle piece disappears also, and as it does the clear space assumes a

radiate structure known as the **sperm-aster**. The head of the spermatozoon is transformed into an elongated nucleus lying to the outer side of the sperm-aster, and the two move together towards the interior of the egg. The path along which the sperm nucleus and aster move determines the plane of the first division of the fertilised egg. While the sperm-nucleus is travelling inwards the egg-nucleus leaves the position it has hitherto occupied at the pigmented pole of the ovum, and also travels inwards to meet the sperm-nucleus at the point which may be described as lying in the axis of the egg at about a quarter of the length of its diameter from the pigmented pole. The centrosome of the spermatozoon disappeared along with the middle piece, but now as the sperm- and egg-nuclei approach a new centrosome makes its appearance in the sperm-aster.

This centrosome occupies a position between the sperm-nucleus and egg-nucleus, and as they approach one another it divides in a direction at right angles to the path along which the sperm-nucleus has travelled. The two centrosomes thus formed diverge from one another and the radiations of the sperm-aster are collected round them to form the polar radiations of the future mitotic spindle. Meanwhile the sperm-and-egg nuclei have increased in size and exhibit changes similar to those of nuclei about to enter upon division. Spindle fibres are formed in connection with the centrosomes and are attached to the two nuclei. Twelve chromosomes now emerge from the reticulum of each nucleus and are attached to the spindle fibres in two distinct and separate groups. Each chromosome is split into halves longitudinally, and the halves are pulled apart and carried to the two poles of the spindle by the fibres. An equatorial plate is formed in the spindle, and the whole ovum divides into two, the segmentation furrow passing through the equator of the spindle and therefore coinciding with the path of entrance of the spermatozoon into the egg. It is noteworthy that this process not only provides for the restoration of the full number of chromosomes but also ensures that each of the two segments or blastomeres into which the egg is divided shall have half of its chromosomes derived from the male and half from the female parent. The importance of this fact in relation to the transmission of hereditary qualities to the offspring cannot be overlooked.

The ovum of the frog, as has been said, is abundantly

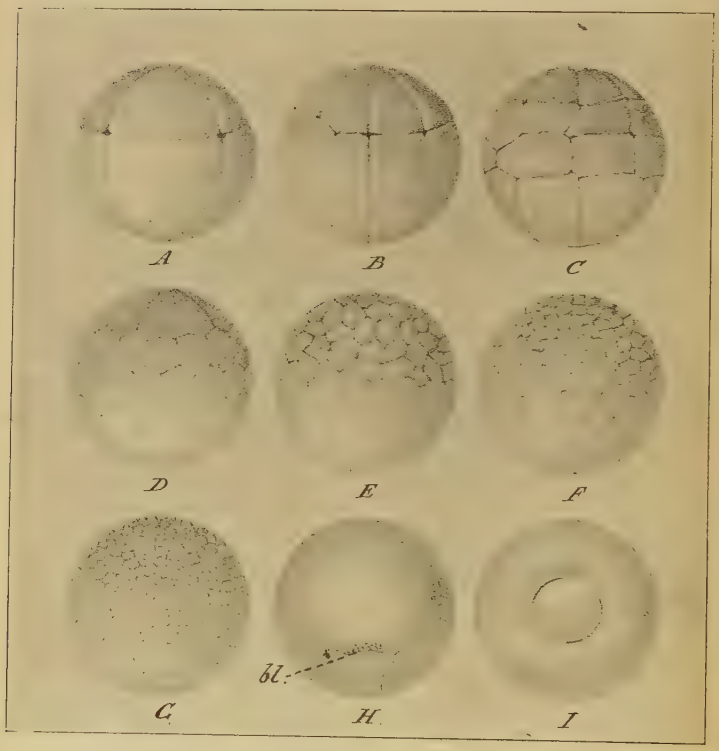

Fig. 27.

Segmentation of the frog's ovum and formation of the blastopore (after Morgan). *A*, eight-cell stage resulting from two meridional and one equatorial divisions. *B*, beginning of sixteen-cell stage. *C*, Thirty-two-cell stage. *D*, Forty-eight-cell stage, showing the smaller cells at the upper pole and larger yolk-laden cells at the lower pole. *E*, *F*, two sides of the same ovum in later stages of segmentation. *G*, a still later stage of segmentation. *H*, the smaller cells are growing over the larger cells but are involuted along a crescentic line *bl*, the dorsal lips of the blastopore. *I*, external view of the blastula, showing the circular blastopore.

provided with food-yolk, stored up chiefly in one hemisphere of the cell. The first segmentation following upon fertilisa-

tion has divided the ovum into two equal halves, or blastomeres. A pause follows, and the ovum divides again, the plane of the second division being at right angles to the first. Thus four blastomeres are formed, each consisting of a smaller upper pigmented protoplasmic part, and a lower colourless part filled with deutoplasm. The third segmentation is described as equatorial, but it does not pass through the equator of

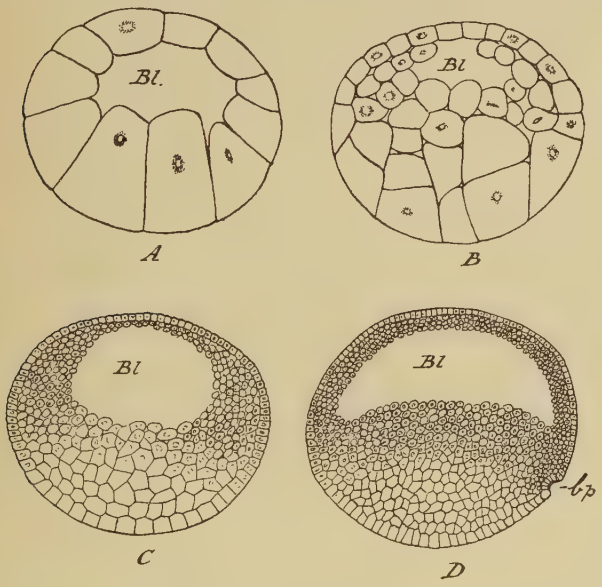

Fig. 28.

A, vertical section through a segmenting ovum at about the stage represented in fig. 26, *D*. *B*, *C*, and *D*, similar sections through later stages. *Bl*, segmentation cavity or blastocœle, *bp*, blastopore. (After Morgan.)

the spherical ovum, but is placed nearer the pigmented pole. It nearly completely cuts off four pigmented upper blastomeres from four lower heavily-yolked blastomeres. Hitherto the planes of division have passed right through the ovum, giving rise to an eight-celled stage, and the next division is described as meridional. Each upper pigmented

blastomere is divided into two longitudinally, and the division lines are continued downwards into the yolk blastomeres. But these, being so largely composed of inert deutoplasm, divide slowly, and their division is completed some time after it has been effected in the upper blastomeres. The next divisions are parallel to the equator, and affect all the sixteen blastomeres, dividing each of them into two, as is shown in fig. 26, *C*. The embryo now consists of thirty-two cells, and the succeeding divisions become irregular, and are no longer synchronous. The upper pigmented cells divide much faster than the lower yolk-cells, and the final result of the first phase of development (usually called the segmentation phase) is a vesicle containing a rather flattened and excentric cavity, whose roof is composed of two layers of small pigmented cells, and the floor of much larger irregularly-polygonal yolk-cells which occupy the whole of the lower hemisphere of the embryo. The small cells pass, without any sharp line of demarcation, into the yolk-cells. Such a hollow vesicle is known as a **blastula**, and its cavity is known as the **segmentation cavity** or **blastocœle**. Further changes, following upon repeated cell-division, result in the formation of a three-layered embryo, and all the organs and tissues of the tadpole, and, finally, of the adult, are derived from these three layers.

The actual formation of the three layers is somewhat obscured in the frog because of the large preponderance of inert food-yolk, and it will be better to defer a consideration of the details of further development till a later stage.

CHAPTER IV

THE RHIZOPODA—AMŒBA PROTEUS

Our studies have hitherto been directed to the elucidation of the anatomy and development of a complex animal provided with tissues and organs which subserve different purposes in its economy, and are modified structurally in accordance with the functions which they have to perform. We have seen that all its tissues (which are comparable to our own) are formed either by, or out of, certain ultimate form-elements called cells, and that the diversity and complexity of the animal's structure is to be referred to the diversity of structure obtaining among its component cells. Further, we have seen that this remarkably complex animal, composed of countless cells, is brought into being from the simplest possible beginning—namely, a germ-cell, which, after undergoing the processes which have been described as maturation and fertilisation, possesses the power of giving rise to the entire organism. The course of the development of the germ-cell has only been lightly touched upon; but we have seen that it consists essentially in the multiplication of the fertilised germ-cell or **oosperm** by division, the products of division cohering and forming a hollow embryo composed of many cells, which are ultimately differentiated to form the tissues of the adult.

We have learned in the course of these studies that all the phenomena of the frog's life (exclusive of its psychical phenomena, which baffle our powers of analysis) are to be referred to the activities of its cells. We now can turn to the study of a large group of organisms of the simplest possible constitution, the Protozoa, whose vital phenomena are manifested within the limits of a single cell.

In commencing the study of the Protozoa, we cannot do better than begin, as is customary, with the study of a common pond animalcule, known to science by the name of **Amœba proteus**. This minute organism, pregnant with meaning to

the biologist, is found in fresh-water ponds and in damp places. There are many kinds of Amœbæ, but that kind known as **proteus** is selected because of its relatively large size and unequivocally simple structure. **Amœbà proteus** is about ·25 mm. ($\frac{1}{100}$th of an inch) in diameter, It is a shapeless mass of protoplasm, which, under moderate magnifying powers of the microscope, appears to be divisible into an outer transparent colourless layer, generally referred to as the ectoplasm, and an inner, more fluid mass, the endoplasm, containing numerous granules of a dark colour. Closer inspection reveals the presence of a small, subspherical, denser body within the endoplasm ; this is the nucleus, and, if the aminal is killed and stained, it is seen, like the nuclei of tissue-cells, to take up the staining fluid with more avidity than the cytoplasm. The nucleus, in fact, contains chromatin, which, in this particular species, is scattered throughout the substance of the nucleus in the form of minute spherules. In addition to the nucleus, clear spaces filled with a watery fluid may be seen in the endoplasm. They are not altogether permanent structures, but are formed or absorbed so slowly that they may be credited with persistent characters, and hence are called permanent vacuoles. Besides these, there is a structure called the **contractile vacuole**. If a living Amœba is carefully watched under the microscope, a clear round space, larger than the permanent vacuoles, is seen to arise in the cytoplasm. It grows in size, just as a soap-bubble grows when blown from the bowl of a pipe, and its optical characters leave no doubt that it is filled with a watery fluid. After reaching a certain size the vacuole ceases to expand, and, after a period of rest, it is suddenly obliterated by the closing in of its walls from all sides. The obliteration of the vacuole is clearly brought about by the active contraction of the cytoplasm forming its walls, and in the process its fluid contents are expelled, though no obvious pores or canals can be seen through which they effect their escape.

These are the only definite organs of the Amœba ; but its most characteristic feature is its constantly-changing shape. The creature, under normal circumstances, is never at rest, but is constantly protruding processes of its cytoplasm, now in one direction, now in another. These blunt, shapeless processes are called **pseudopodia**, and the characteristic move-

ment produced by their extension and retraction is called amœboid movement.

Careful observation of pseudopodial movement shows that the formation of a pseudopod is initiated by a bulging of the hyaline edge of the cytoplasm. The bulge increases in size and for a while the internal granular endosarc is not affected. Then, rather suddenly, the granular mass seems to flow into the hyaline process. The granules flow forward, rapidly in

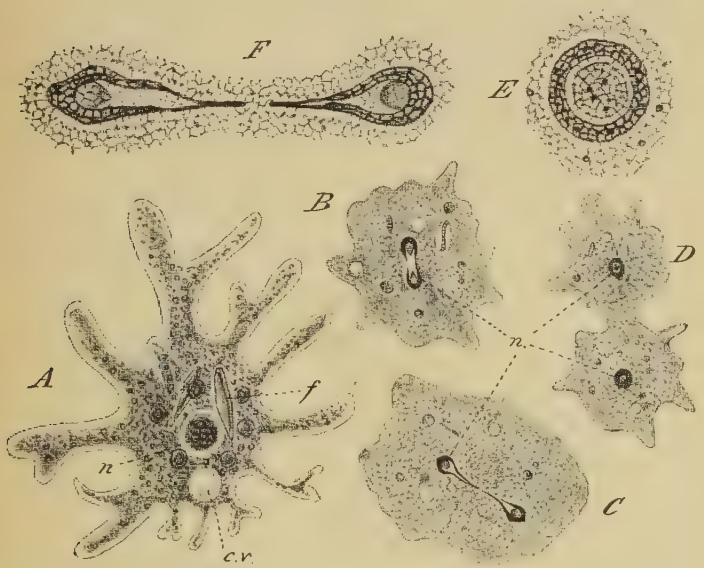

Fig. 29.

A, *Amœba proteus*; *n*, nucleus; *c.v.*, contractile vacuole; *f*, a diatom enclosed in a food vacuole. *B*, *C*, *D*, three successive stages in the division of *Amœba crystalligera*, showing the amitotic division of the nucleus. *E*, resting nucleus of *Amœba crystalligera*, highly magnified, showing the central so-called nucleolus surrounded by an envelope of chromatin. *F*, dividing nucleus of the same species, highly magnified. (*A* after Leidy; *B-F* after Schaudinn.)

the middle but usually more slowly at the sides, and as they reach the extremity of the growing pseudopod they spread out so that some of them approach its lateral borders. They then stop while the central part of the stream moves on

following the advancing hyaline extremity of the pseudopod, until a large lobate process is formed, as large it may be as the whole of the remaining body of the Amœba. Continued formation of pseudopodia in one direction leads to locomotion in that direction, but the movement is seldom definite in *Amœba proteus*. After any given pseudopod has attained to a certain size it ceases to extend; the streaming of the granules into its interior is arrested, and eventually the flow is reversed. Another pseudopod has been forming in some other direction, and the granular endoplasm streams off into it, the older pseudopod diminishing in size and eventually becoming obsolete. There are other species however, of which *Amœba limax* is an example, in which progression is more definite. This animalcule does not put forth branching pseudopodia from all parts of its body, but is constantly pushing forward a broad hyaline process from one end of its somewhat elongated body. The granular ectosarc flows forward into this process, and as the latter is continually advancing and being filled by the granular stream from behind, the whole body travels forward in a definite direction. It has been shown by means of a simple experiment that the streaming movement is accompanied by a rolling action of the whole body. If particles of soot are dropped on the Amœba, some will adhere to its upper surface, and any given particle thus attached may be seen to pass slowly forward to the anterior edge of the advancing animalcule. It passes round this edge to the lower surface and there stops still until the whole body of the Amœba has passed over it and it has come to lie beneath the posterior end. It then mounts upwards again to the upper surface, is carried forward to the anterior edge, goes underneath it again and so on as long as the animalcule is in movement. Occasionally particles of sand or diatoms are imbedded in the outer layer of the cytoplasm, and these exhibit the same movements as the particles of soot attached to the surface, showing that the ectosarc takes part in the slow rotatory motion. This method of progression can be imitated by partially distending a thin indiarubber bag and rolling it along a table. A spot marked on the upper surface of the bag will be seen to behave like a particle of soot attached to the upper surface of the Amœba. Under certain conditions similar movements

accompanied by a similar streaming of the internal granules can be induced in droplets of various fluids in which solid particles are suspended. For instance a drop of glycerine impregnated with soot and immersed in oil may be made to move in this manner over a piece of cardboard a portion of whose surface has been wetted to prevent the oil soaking into it. This experiment and others of a like nature have led many people to believe that the movements of Amœbæ can be explained on simple chemical and physical grounds, and some of the theories proposed are at least partly justified by the remarkable analogies observed between the behaviour of artificial mixtures and the living organism.

There is also a striking analogy between the structure of protoplasm and that of certain artificial emulsions. It can be shown that in many Amœbæ the cytoplasm, including both ectoplasm and endoplasm, has the structure of an exceedingly fine sponge-work, or rather, let us say, a foam. Imagine a foam or froth composed of bubbles of extremely minute size. Imagine that the skins of these bubbles are composed of a somewhat denser tenacious material and that their cavities are occupied, not by air, but by a fluid of less density. The bubbles in the centre of the froth would be polygonal through mutual pressure, and if the whole thing could be hardened and cut into slices the sections of the walls of the bubbles would look like a network having somewhat irregular polygonal meshes. Such a foam may be made by mixing finely-pounded common salt with thick rancid olive oil. A small droplet of this mixture, placed in water and examined under the microscope, exhibits a structure marvellously like that of the cytoplasm of an Amœba. It is also divisible into an outer more hyaline border and an inner granular mass, and it has been shown that the outer hyaline border is due to the special form assumed by the alveoli or bubbles in consequence of the surface tension produced by the contact of two immiscible liquids of different densities. A similar arrangement is found in the hyaline border or ectoplasm of an Amœba and it is permissible to assume that the similar effects observed in the two cases are due to like causes. It has further been shown that if the surface tension be reduced at any point of the droplet of salt and oil a streaming movement of its contained granules will be set up in the

direction of that point, and a pseudopod-like process may be emitted. The streaming movements in the droplet, however, are different from those observed in an Amœba, and in this as in all other attempts to identify vital with simple physico-chemical processes, the comparison breaks down under the test of rigorous criticism. The droplet of oil and salt does not ingest food, does not assimilate, does not grow and reproduce its kind. The most essential vital phenomena are wanting and it cannot be said, in any sense, to live. Moreover, if watched for a long time, the movements of an Amœba are seen to be of a purposive character—that is to say, they are clearly adapted to the necessities of the organism, as is evident when an obstacle is met with, or when the animalcule endeavours to seize and ingest some object that rolls away from it, or attempts to capture a smaller member of its own kind for food.*

Like all indisputable animals an Amœba takes into its interior or, as we say, *ingests* solid food, consisting of vegetable or animal matter, Oscillaria, Diatoms, and even other Protozoa. These substances may generally be seen in the central part of the cytoplasm, and careful examination shows that each separate morsel of food is enclosed in a space filled with fluid, called a **food-vacuole**. The vacuole however is formed subsequent to the ingestion of the food, and is not merely a droplet of water taken in along with it, but a secretum of the protoplasm. There is no special orifice nor even a soft spot in the protoplasm where solid food is taken in. The pseudopodia come into contact with some food-substance; they embrace it, flow round it, meet above and below it, and finally enclose it. Blochmann has described how *Amœba proteus* catches the agile infusorian *Cyclidium glaucoma* in this simple manner. The Cyclidium seems to be fatally attracted to the Amœba, swims towards it, and lies between its pseudopods. In this position it is enclosed above and at the sides by the flowing movement of the protoplasm; it seeks awhile to escape from the death-chamber, but it is finally enclosed; and, when enclosed, a vacuole is secreted

* For a further account of the movements, habits and reactions of Amœba, the reader should consult the very interesting work of H. S. Jennings, "Contributions to the Study of the Behaviour of the Lower Organisms." Published by the Carnegie Institution of Washington, 1904.

round it. It is evident that the walls of the death-chamber, formed of fused pseudopodial processes, were originally part of the external layer or ectoplasm, and that in enclosing the Cyclidium or other prey they have become internal, and are eventually merged into the inner substance, or endoplasm, of the Amœba. Thus ectoplasm can become endoplasm and *vice versâ*. It would not, however, be correct to say that all Amœbæ consist of naked protoplasm without any external limiting coat. **Amœba bi-nucleata**, so named because it has two nuclei, is a form with a distinct though very thin pellicle outside the external alveolar layer, and this pellicle may be made evident by certain dyes. **Pelomyxa palustris**, a very large and rather peculiar Amœba, is covered all over with minute non-vibratile hair-like appendages; and **Amœba villosa** has a tuft of similar appendages at one end of its body, pseudopodia of simple form being formed only at the opposite end.

It has been demonstrated that the contents of the food-vacuoles, at the time of their formation, are acid, and eventually they exercise a solvent action upon proteid substances, but not, it would seem, upon starches and fats. It is most probable that the fluid contents of a food-vacuole are a special secretion of the protoplasm, containing a ferment or enzyme, which has an action analogous to that of the gastric secretion of higher animals. The proteid morsel enclosed in a food-vacuole is gradually dissolved, and disappears, only a small granular residue remaining. This residue is eventually rejected together with other non-nutritious substances that have been taken in, as it were, accidentally. There is no special aperture for the ejection, as there is none for the ingestion of solid matter. One may say that the Amœba flows away from its indigestible contents, leaving them behind.

Since Amœbæ live in muddy and sandy bottoms amidst all sorts of inorganic non-nutritious grains and fragments, it is clear that they must exercise some sort of selection in ingesting solid matter; for if they did not they would take in every particle of convenient size that they meet, and they do not. Moreover an Amœba living in water that contains numerous diatoms of relatively large size may be seen to engulf a number of these apparently inconveniently large objects

almost to the exclusion of other substances, thus making a discrimination between things good for food and things not good. But its powers of discrimination are not great, for it will sometimes ingest grains of quartz sand, or such non-nutritious substances as powdered carmine, or powdered litmus. None the less we must credit the animal, lowly as it is, with a certain power of selection which constitutes a part of its sensibility or irritability.

In common with all living things the Amœba exhibits that response to external stimuli which we call irritability. Thus its movements are retarded by cold and up to a certain point are made more active by heat. But if the temperature of the water in which it is contained is raised above this point, its movements become less active and cease altogether between 30° and 35° C., but begin again when the temperature is lowered. At about 40° C. the protoplasm is coagulated and the Amœba is killed. The organism is also responsive to mechanical, chemical, thermal, and electrical stimuli. It is possible to draw out a glass rod to so fine a point that it may be used to prick or stimulate any desired part of the Amœba's body. If such a point be thrust into the advancing end of an Amœba, the forward movement is at once arrested; the ectosarc of the region stimulated contracts, but the forward streaming movement of the granular endosarc continues for a short time, causing a bulging of the middle of the body. Then the ectosarc is protruded at some point removed from the area of stimulation, the current of granules is reversed and a new pseudopod is formed, and the animal starts off on a new course, generally at right angles to the old one. In this case the stimulus is a strong one, and the Amœba moves away from it. This is called a *negative* reaction. But if the stimulus is weak, a *positive* reaction follows. Thus an Amœba moving along a surface may be seen to turn towards small objects with which it comes in contact by its advancing end. A negative reaction follows when chemical or thermal stimuli are applied to one side of the body, the phenomenon being essentially the same as in the case of a strong mechanical stimulus. For example, if a minute drop of methylene blue or other chemical is brought into contact with the advancing end of an Amœba by means of a fine capillary tube, movement in that direction is arrested, and a new pseudopod is

formed, often at the opposite end of the body. The effect of an electrical stimulus is clearly marked. If an Amœba is placed in a drop of water between the electrodes of an induction battery, and a single weak shock is passed, it may be seen to withdraw its pseudopodia and contract itself into an irregularly shaped lump, gradually recovering its form and resuming its pseudopodial movement after the effects of the shock have passed away. But if subjected to a constant current the effects are different. At the make of the current the Amœba contracts in the same way as under the influence of a single shock, but immediately recovers, emits pseudopodia in the direction of the kathode, and continues to move in this direction as long as the current passes. If the current is reversed so are the movements of the Amœba. On the break of the current, the animal contracts as before, and after a short time resumes its normal movements.

There is also evidence that Amœbæ are sensitive to light, though experiments in this direction have been so far unconvincing. But *Pelomyxa palustris* has been observed to avoid the light, creeping under the mud at the bottom of the vessel in which it was confined during the day, and crawling out on the sides of the vessel during the night. In these diurnal migrations the animalcule traversed a distance of 20 cm. during the twenty-four hours. On the introduction of water-weeds into the vessel the Pelomyxæ were seen to crawl up them during the night, and on being suddenly exposed to bright sunlight they contracted themselves into balls and dropped off the weed to the bottom of the vessel, where they hid themselves under the mud. But after the water-weed had been in the vessel for some time the Pelomyxæ no longer left the mud but stayed buried in it both by day and night. It would seem that, before the introduction of the water-plant, the water became deficient in oxygen, and that the deficiency was greatest in the mud at the bottom of the vessel. During the day the animalcule's aversion to light proved stronger than its intolerance of an insufficient supply of oxygen, so it remained buried in the mud, but during the night left its hiding-place in search of oxygen. When the whole contents of the vessel became appropriately oxygenated the migration ceased.

Thus Amœba, simple as its constitution is, exhibits the

characteristic vital phenomena of irritability, automatism, assimilation, and excretion. We cannot doubt that it is also metabolic. The pseudopodial movements are manifestations of energy; they imply waste of material, and we can infer from the fact that the animalcule takes in and digests food that the waste of its substance is made good by the elaborated products of digestion. In so small an organism the actual processes of waste and repair cannot be followed out in detail, none the less we can assert that they are performed. So, too, we can assert that the Amœba is respiratory, that the energy exhibited in pseudopodial movement is the result of the oxidation of the tissues, and that one of the waste products is carbon dioxide. There is no definite respiratory organ, unless, indeed, the contractile vacuole functions as such, and the amount of carbonic acid gas given off is too small to be collected and measured. But the same observation which showed that Pelomyxa is sensitive to light shows also that it requires oxygen.

Lastly, Amœba is reproductive. Under normal conditions, when food is abundant and the temperature sufficiently high, it propagates its kind by the simple method of binary division, but under less favourable circumstances by a more complicated process known as encystment with spore formation. It is difficult, however, to give a precise account of the life-cycle of any one species of Amœba, for it is a remarkable fact that, although it is one of the commonest objects of study, the reproductive processes of this animalcule have been but rarely seen and described. It is even now uncertain whether mitotic or amitotic division of the nucleus during binary division is the more common. It is at all events certain that amitotic division does occur. In *Amœba crystalligera*, the nucleus consists of a central mass or kernel, which stains but feebly with ordinary dyes and has been considered as the equivalent of a nucleolus. Around this kernel is an envelope of material which stains deeply and is undoubtedly chromatin. Outside this again is a cortical layer which scarcely stains at all. The characteristic alveolar structure of protoplasm is distinguishable in all three components of the nucleus (fig. 29, *E*). When division is about to take place the nucleus, previously spherical, becomes oval and is eventually drawn out into an elongated dumb-bell shape (fig. 29, *C* and *F*), all three layers sharing in

the elongation without obvious change. The connecting thread between the two swollen ends of the nucleus becomes attenuated and finally snaps, upon which the two ends round themselves off and become new nuclei. At the same time a deep constriction appears in the cytoplasm, passing towards the place where the nuclear thread divided. This constriction deepens and eventually divides the body of the Amœba into two halves, each containing one half of the original nucleus. In this case there is no trace of centrosomes, spindle, chromosomes or astral rays, and the division is undoubtedly amitotic. But in *Amœba bi-nucleata*, a primitive kind of mitosis has been observed. In this species there are two nuclei which act together and undergo the same changes during division, in such a manner that each daughter Amœba has two nuclei, one derived from each of the two nuclei present in the parent form. The nuclei have very firm nuclear membranes, and inside them a nuclear sap containing numerous chromatin masses. In the prophase of mitosis the chromatin masses break up, and their minute fragments are scattered through the substance of the nucleus. The nucleus itself becomes somewhat flattened, and at each of its two flatter poles a small mass of hyaline structureless protoplasm, apparently the representative of the centrosphere, makes its appearance as a flat cap. Meanwhile the chromatin granules collect in the equatorial plane of the nucleus and form a plate. A true spindle has not been observed, but in the later stages of division, fine longitudinal threads were seen stretching between the chromatin particles, now separated into two groups, of which one travels towards each pole of the nucleus. After the separation of the chromatin groups, the two nuclei divide to form four, and division of the cell-body follows. Indications of mitosis have been described in the binary division of *Amœba proteus* and *A. verrucosa.*

Encystment, followed by the sub-division of the body into a number of minute reproductive bodies or spores, has been observed only once in *A. proteus.* In this case the encysting Amœbæ were kept under observation in a laboratory during the winter, and the whole process occupied from two and a half to three months. Before encystment the animals withdrew their pseudopodia and assumed a spherical shape. The streaming movements of the endoplasm became slower and

eventually ceased; at the same time the large albuminous granules seemed to dissolve and the whole cytoplasm became minutely granular, all distinction between ectoplasm and endoplasm being lost. After a period of rest the streaming

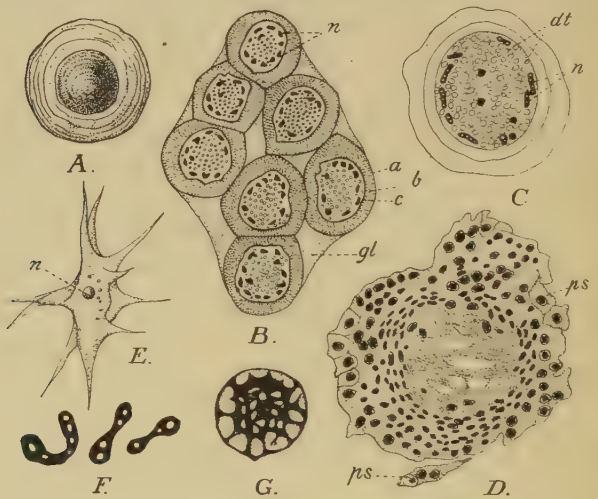

Fig. 30.

A, a single reproductive cyst of *Amœba proteus*, magnified about 60. *B*, a section through a group of seven cysts of *A. proteus*, ×60. *C*, a section through a single cyst, ×about 180. *D*, a section through a cyst with some 600 nuclei showing the differentiation of the pseudopodiospores at the periphery of the cyst; the cyst-wall is not represented; ×about 200. *E*, a single free pseudopodiospore; ×about 175. *F*, dividing nuclei of a cyst, showing dumbbell-shaped and horseshoe-shaped forms; ×625. *G*, one of the peripheral nuclei from D; ×750: the nuclear membrane is distinct, and the chromatin collected in the centre of the nucleus. *a*, *b*, *c*, outer, middle and inner layers of the cyst-wall. *dt*, granules of reserve material or deutoplasm. *gl*, gelatinous investment holding the cysts together. *n*, nuclei. *ps*, pseudopodiospores. (After Scheel.)

movements began again, and the Amœba rotated slowly and continuously about its centre, first in one direction, then in another, but without changing its position. As it rotated it formed a thin coat or cyst-wall, as a secretion from its outer surface, and the nucleus divided several times by amitotic divisions. A single specimen was observed to rotate in this manner for four days, at the end of which time about twenty

highly refractive, round or oval, vesicular nuclei were present. The cyst-wall did not share in the rotation but gradually became thicker by the addition of new layers to its inner surface. By the fifth day the rotatory movement had ceased, and shortly afterwards some thirty nuclei were counted, and the cytoplasm was full of refractive albuminous spherules. The nuclei apparently consisted of corpuscles of plastin encased in chromatin, and in division they simply became elongated and dumbbell-shaped, and divided into two. The albuminous spherules persisted in cysts in which some 300 nuclei were present, but then began to disappear, and were no longer to be seen in cysts containing from 500 to 600 nuclei. Throughout these phases the dividing nuclei had no membrane, but when about 600 were formed they acquired membranes and passed to the periphery of the encysted Amœba. At the same time each nucleus became round and vesicular and the chromatin was collected into its centre. The cytoplasm surrounding each nucleus was then segmented off as a minute corpuscle which presently began to put forth pseudopodia and escaped through the cyst-wall which was now in a state of disintegration. The segmentation did not extend to the centre of the encysted animal, which was left behind a sa mass of residual protoplasm. The young forms or spores on escaping from the cyst appeared as perfect amœbulæ; they were transparent, contained very few granules, put forth many pointed pseudopodia, and measured from ten to fourteen thousandths of a millimetre in diameter. Though very different from the adult form at the time of their emergence, these amœbulæ, when supplied with appropriate food, could be reared into the adult *A. proteus*. The cysts were either single, or several of them were aggregated together and invested by a common gelatinoid mass, derived from the outer walls of the cysts. No conjugation was observed, either between the Amœbæ prior to encystment or between the amœbulæ liberated from the cysts, and it is noticeable that the young forms were amœboid from first to last, and never showed any trace of a flagellate condition. Minute amœboid reproductive bodies such as these are often spoken of as **pseudopodiospores.**

Several other Rhizopods allied to Amœba have been

observed to encyst and divide into a number of minute young forms which are subsequently set free by rupture of the cyst-wall. *Paramœba eilhardi*, a form closely allied to Amœba, encysts and divides into a number of segments which emerge from the cyst as minute bean-shaped, actively swimming bodies, each provided with a pair of long vibratile protoplasmic filaments termed **flagella**. These **zoospores**, as they are called, divide with nuclear mitosis, and eventually lose their flagella and become amœboid, but they have not been observed to conjugate.

The large and peculiar multi-nuclear Rhizopod, *Pelomyxa lacustris* has an interesting life-history, culminating in the formation of a number of pseudopodiospores, which for a while put forth pseudopodia, ingest food and lead an independent existence, but are incapable by themselves of growing up into the parent form. To this end it is necessary that two pseudopodiospores (also called **gametes**, from the Greek γαμέτης, a spouse) should conjugate. They come together and fuse completely, nucleus with nucleus and cell-body with cell-body. The resulting individual is known as a **zygote** (ζυγωτός, joined together), and develops into an adult Pelomyxa. The reproductive processes in this organism are heralded by peculiar nuclear changes, the details of which are too complicated to be dealt with in this place, but it is an interesting and significant fact that prior to the formation of the pseudopodiospores or gametes, each of the many nuclei contained in the parent Pelomyxa undergoes two mitotic divisions, in which definite chromosomes make their appearance. The first of these is a meiotic or reducing division, the second an equal division, but with half the number of chromosomes that made their appearance in the first division.*

It is obvious that the conjugation of the two gametes is strictly comparable to the fertilisation of an ovum by a spermatozoon, and that the preparatory nuclear changes are similar in each case. In other words, in an organism that is indisputably a Protozoon of simple structure, we find a fully differentiated sexual process, essentially the same as that described for the frog, and differing from the latter chiefly in the fact that the two gametes are equal in size and indistinguishable

* K. Bott, Ueber die Fortpflanzung von Pelomyxa lacustris. Archiv für Protistenkunde viii. 1907

in appearance, so that a male cannot be distinguished from a female form.

The formation of gametes is not preceded by encystment in Pelomyxa. The zygote resulting from conjugation frequently encysts, but this is simply a protective measure, and has nothing to do with reproduction. Similarly an Amœba may often be seen to encyst itself and pass into a resting stage, but after a time the cyst-wall is absorbed, the Amœba emerges and resumes its active existence. There is therefore no necessary connection between encystment and reproduction.

Amœbæ and their allies, distinguished from other Protozoa by the possession of pseudopodia, are classed together as Rhizopoda. Amœba is one of the most simple members of the group, and may be taken as a type of it, but it must not be supposed that all Rhizopoda have so simple a structure. Some of the nearest allies of Amœba having, like it, blunt lobose pseudopodia, have the power of forming shells of characteristic form for the protection of their bodies. Thus **Difflugia**, a common fresh-water Rhizopod, protects itself by a case formed of particles of sand glued together by a secretion of the protoplasm. **Arcella**, another common fresh-water form, has a watch-glass-shaped shell formed of a chitinoid substance. The concavity of the watch-glass is covered in by a plate with a central hole through which the pseudopodia are protruded. Not far removed from these, and differing from them chiefly in the fact that their pseudopodia are long and thread-like, frequently branched at their extremities, and anastomosing so as to form a protoplasmic network outside the cell-body, are **Euglypha**, a fresh-water Rhizopod, with an ovoid shell formed of hexagonal siliceous plates, and **Microgromia** with a chitinous shell which is not made up of plates, but is continuous. Closely allied to these, again, are the Foraminifera, a very large group of rhizopodous Protozoa, with calcareous shells, many of which are of great beauty and complexity. The Foraminifera are all marine, and are extremely abundant. Some of them are pelagic—that is to say, they float at or near the surface in the open ocean far away from land; and the bottoms of those oceans whose depth does not exceed 2000 fathoms are generally covered with deposits of a grey mud, which is chiefly composed of the calcareous shells of the countless Foraminifera which have

lived and died in the waters above. At depths greater than 2000 fathoms, the proportion of Foraminifera in deep-sea deposits becomes less and less, and at great depths the deposits are largely composed of the siliceous skeletons of another class of marine Rhizopoda, the **Radiolaria**. In the greater depths the fragile calcareous shells of the Foraminifera have been dissolved by the action of the carbonic acid dissolved in the sea-water; it seems that the solvent action is greater the greater the pressure. But the flinty skeletons of the Radiolaria are not dissolved, and hence they take the place of the Foraminifera at great depths. There are, of course, Radiolarian skeletons amongst the calcareous deposits in moderate depths, but they are scarcely distinguishable among the greatly preponderant mass of calcareous shells. The chalk, which in some parts of England is over a thousand feet in thickness, is almost entirely composed of the shells of Foraminifera, and in the Barbadoes there are deposits of considerable thickness formed almost entirely of the flinty skeletons of Radiolaria.

It is beyond the purpose of this book to enter into details concerning all the different groups of the Rhizopoda, however important they may be from a geological point of view. But the reader should remember that animalcules whose structure, except for the presence of a calcareous or flinty skeleton, is scarcely more complex than that of an Amœba, have played and are still playing a very important part in the formation of the earth's crust.

CHAPTER V

THE SUN ANIMALCULE

ACTINOSPHÆRIUM EICHORNII

In many freshwater pools, particularly in the warm months, a number of glistening white specks, about as large as the head of a small pin, may be seen floating in the water. Examined under the microscope each of these specks is found to be an animalcule having the structure represented in fig. 31. It has a spherical protoplasmic body, from which radiate out on all sides a number of stiff ray-like processes, the pseudopodia, whence the animal derives its name Actinosphærium (ἄκτινος, a ray; σφαῖρα, a sphere). Examined more closely, the spherical body is seen to be composed of naked protoplasm, so richly beset with clear spaces or vacuoles that the animal may not inaptly be compared to a speck of foam. It must be borne in mind, however, that the vacuoles of Actinosphærium differ from foam bubbles in containing not air but fluid. When viewed by reflected light Actinosphærium appears brilliantly white, because of the reflection of light from all parts of its body, and the details of its organisation cannot well be distinguished, but when examined by transmitted light, especially if it be subjected to gentle pressure, the details of its structure can easily be made out. The body is then seen to consist of a peripheral or cortical lighter and more transparent layer called the **ectosarc**, and a central darker medullary portion called the **endosarc**. The difference is really due to the size of the vacuoles, which are large and bounded by very thin envelopes of granular protoplasm in the ectosarc, but are smaller, with much thicker protoplasmic walls, in the endosarc. The protoplasm of the endosarc shows a further difference in that it is more granular, and therefore less transparent, than that of the ectosarc. In any collection of Actinosphæria there is a considerable difference in size between individuals.

They vary from 0·4 to ·04 mm. in diameter. The smaller are the younger forms, and in them the large vacuoles of the ectosarc form a single peripheral layer, separated by thin radial walls of protoplasm. In the larger and older forms the

Fig. 31.

Actinosphærium Eichornii, viewed by reflected light, showing the radiating pseudopodia, the lighter ectosarc, and the darker central endosarc containing numerous nuclei. Two contractile vacuoles are seen on the edge of the ectoplasm.

vacuoles of the ectosarc are generally two or three layers deep.

Even in the living animal, but more easily in one which has been killed with osmic acid and stained with picrocarmine, one can distinguish a number of minute spherical bodies, deeply stained by picrocarmine, each of which contains a more darkly stained central spot. The spherical bodies are the nuclei, the central spots their nucleoli. The nuclei are always numerous, but more numerous in the larger and older than in the smaller and younger animals. In the former

as many as 150 may be present, and some authors describe an even larger number. The nuclei always lie in the more peripheral part of the endosarc, never in its centre or in the ectosarc. This constant position of the nuclei is indicative of a differentiation between the protoplasm of the ectosarc and endosarc; a differentiation which is also expressed in the more granular appearance of the latter. Further, we find that the processes of digestion are accomplished wholly in the endosarc. Actinosphæria, like all true animals, ingest solid food, and in any specimen one may observe foreign bodies, infusoria, diatoms, algæ, etc., lying in the endosarc and surrounded each by a food-vacuole. The formation of food-vacuoles has not been studied with the same care in Actinosphærium as in Amœba, but their form and optical characters differ from those of the ordinary permanent vacuoles with which the body is beset, and there can be little doubt that, as in Amœba, each food vacuole is secreted round the solid particle contained in it. That the contents of the food-vacuoles exercise a solvent action upon the diatoms, infusoria, and other bodies taken in as food is shown by the various stages of disintegration exhibited by the latter. The darker more granular constitution of the protoplasm of the endosarc is doubtless due in large part to its being loaded with the products of digestion. The endosarc, then, is the seat of the digestive processes, and it may be remarked that the fact that these processes are here carried on in the same region as that in which the nuclei are found, confirms the conclusion supported by many other facts, that the nucleus plays an important part in the function of assimilation in the cell.

In order that we may understand the manner in which Actinosphærium captures and ingests its food, which, it must be remarked, consists of active living organisms, we must first consider the structure and action of its pseudopodia. They are not, like those of Amœba, of constantly changing form, nor are they blunt and lobose, but are semi-permanent structures radiating outwards in every direction, like fine needles. Careful examination with a high power of the microscope shows that every pseudopod is provided with a very slender axial filament or rod which runs down its centre, passes through the ectosarc, and ends, at some considerable

distance from the centre of the body, in the endosarc. These needle-like supports of the pseudopodia form the skeleton of the animal. They end peripherally in extremely fine points; proximally they are somewhat thicker, and their internal ends are wedge-shaped. They give the stiff ray-like appearance to the pseudopods; but they are not stiff, but elastic and easily bent, being formed of an organic substance which has been called elastin. This substance may be absorbed by the protoplasm and the whole pseudopod withdrawn, and if the pseudopod is again protruded its axial rod is reformed. The radiating rods are clothed with a layer of protoplasm, thickest at the base of the pseudopod, and tapering to a very fine thread at its end. The protoplasm does not invest the skeletal rod as an even coat, but here and there it may show swellings and prominences which come and go, and it may easily be seen, on close examination, that the protoplasm of the pseudopods exhibits the streaming movements which have already been described as characteristic of the protoplasm of many cells. Granules may be seen floating up one side of a pseudopod and down the other; and a similar streaming of granules can be seen in the protoplasmic walls of the vacuoles, both of ectosarc and endosarc. If some small and active infusoria are introduced into the drop of water in which an Actinosphærium is imprisoned under observation, its mode of catching and ingesting its prey may be seen. When the infusorian swims among the pseudopods and touches them they bend suddenly inwards so as to enclose it in a trap; the infusorian struggles for a while, but appears soon to be paralysed, though it is not clear why it is. As its struggles become less violent, knots of protoplasm appear on the distal extremities of the pseudopodia enclosing it, and these travel centripetally down the axial filaments, drawing the infusorian with them till it reaches the ectosarc into which it is passed, and so through the ectosarc into the endosarc where it is surrounded by a food-vacuole. Food may be ingested at any part of the body, and it is evident that the stiff radiating pseudopodia form a trap-like apparatus, enabling the inert-looking Actinosphærium to capture organisms much more agile than itself. The active bending movements of the pseudopods are manifestations of the contractility of the protoplasm, and contractility is further exhibited by the

ectosarc ; this, when the animal is subjected to a weak electric shock, a sudden jar, or other stimulus, may be seen to contract, diminishing the size of the vacuoles, which, as the effects of the stimulus pass away, recover their normal dimensions.

An Amœba, as we have seen, possesses a single contractile vacuole which is credited with excretory functions. Actinosphærium has two or more contractile vacuoles, situated superficially on the surface of the ectosarc. They expand slowly, swelling till they project like bubbles from the surface of the body, and then their outer walls collapse inwards, expelling their fluid contents, though no definite channels for their escape can be observed. At times two or more Actinosphæria may be seen to come into contact, and their pseudopodia fuse together. The process of fusion goes on until their bodies come into contact and also fuse, so that a double individual or a colony of several partially-fused individuals is formed. This phenomenon has been called **plastogamy.** Its significance is doubtful ; no fusion of the nuclei has been observed to accompany the fusion of the cytoplasm of the cell-bodies, nor does the phenomenon appear to be in any way connected with reproduction, so it cannot be regarded as a process of conjugation, such as will be more particularly described in other Protozoa.

Normally Actinosphærium reproduces itself by binary division, and a celebrated observer of the life-histories of Protozoa states that if a number of these animalcules are kept without food for a time, and are then provided with a superabundance of food in the shape of the common ciliated infusorian Stentor, they multiply rapidly by division. In binary division the globular body is simply divided into two halves by a constriction, each half containing a number of nuclei. But both before and after division the number of nuclei is constantly increasing by mitotic division. The mitosis, however, differs from that which has been described as typical for the cells of multi-cellular animals, and since it may be regarded as a type of the modified form of mitosis characteristic of Protozoa, it will be worth while to consider it in some detail.

The resting nuclei present some variety of form, but they may in general be described as spherical bodies from ·012 to

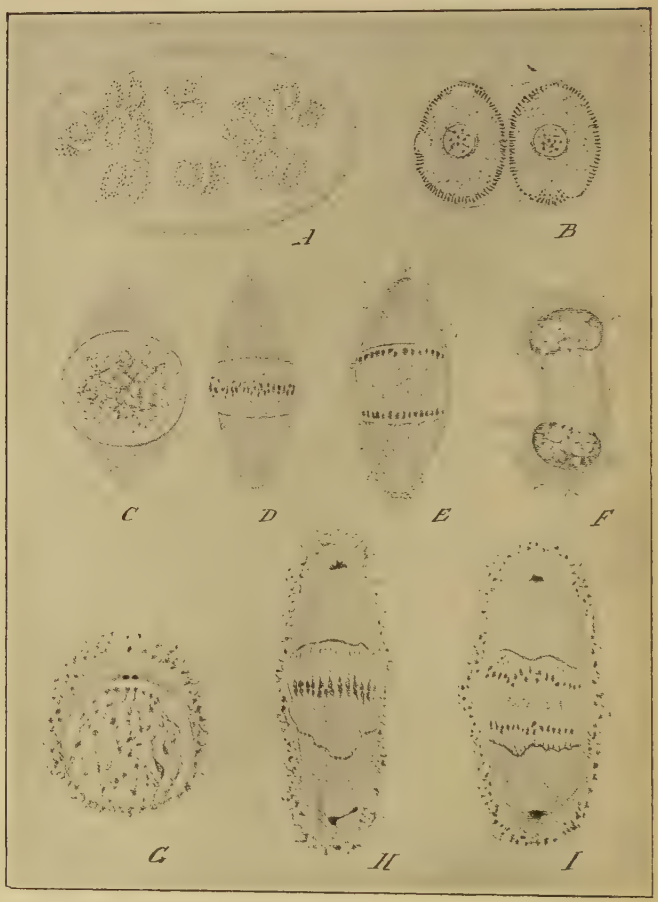

Fig. 32.

A, encysted Actinosphærium, the primary cysts dividing to form secondary cysts. *B*, a pair of secondary cysts, more highly magnified, showing the coat of siliceous spicules; the nuclei are in the resting stage previous to division to form the polar bodies. *C*, normal mitosis of a non-encysted Actinosphærium showing the plasmatic cones. *D*, *E*, *F*, successive stages of normal mitosis. *G*, resting nucleus of a primary cyst, the centrosome dividing preparatory to mitosis. *H*, *I*, successive stages of mitosis in a secondary cyst during the formation of the polar bodies. (After R. Hertwig.)

·018 mm. in diameter consisting of a nuclear membrane, a network of achromatic (*i.e.* not easily stainable) substance, containing a more fluid substance in its meshes, and a single, relatively large deeply-staining karyosome consisting of two different substances, namely chromatin and a material which stains differently to chromatin, forms the true nucleoli of tissue-cells, and is called **plastin**. The karyosome of Actinosphærium varies very much in shape, being sometimes compact and oval or crescentic, sometimes stellate, variously branched, or broken up into minute chromatin particles which are scattered through the nucleus. When a nucleus is about to divide, conical accumulations of homogeneous cytoplasm make their appearance at two opposite poles, forming the so-called plasmatic cones. The nucleus, previously spherical, becomes flattened between the plasmatic cones, so as to be shaped like a bi-convex lens (fig. 32, *D*). Meanwhile the chromatin of the karyosome has become distributed along the threads of the achromatic network in the form of branching strings of minute granules. At the same time peculiar structures known as the **polar plates** make their appearance at the two poles of the nucleus underlying the bases of the plasmatic cones. These polar plates are thin curved plates of a homogeneous, highly-refracting, nuclear substance, and it should be noticed that they arise **inside** the nuclear membrane, and cannot therefore be homologised with the archoplasm nor yet with the centrosome of tissue-cells. Similar pole-plates have been observed in the dividing nuclei of *Amœba bi-nucleata*, in Euglypha, Paramecium and several other Protozoa. The meshes of the achromatic network now become elongated and stretched between the two pole-plates to form the achromatic spindle (fig. 32, *E*). When the spindle is established the chromatin granules, previously distributed along the meshes of the achromatic network, become aggregated at the equator of the spindle in the form of numerous little lumps or rods of irregular shape, each of which may be regarded as a chromosome. Each chromosome divides into halves which diverge from one another to the opposite ends of the spindle, there to form by fusion with their fellows two continuous plates of chromatin underlying the pole-plates (fig. 32, *F*). The achromatic spindle, and with it the whole nucleus, have meanwhile become elongated, and finally a constriction divides the

nucleus into two equal halves, each of which contains a pole-plate, a half of the spindle, and a chromatic plate. From each half a daughter-nucleus is reconstituted. This description only applies to the nuclear division of free living Actinosphæria; in the processes about to be described three other varieties of mitosis have been observed, the details of which need not occupy our attention except in so far as they are of importance for the understanding of the phenomena under consideration.

At the onset of winter Actinosphærium ceases to multiply by binary fission, and undergoes a process known as encystment with spore formation. The axial filaments of its pseudopodia are absorbed; the pseudopodia themselves are withdrawn; the vacuoles in the cytoplasm disappear; and a gelatinous, sticky envelope of relatively considerable thickness is secreted as a protective coat to the protoplasm. A number of round or oval platelets, or granules with thickened edges, make their appearance in the cytoplasm, rendering it turbid and opaque. These granules seem to serve as reserve material for the spores which are shortly afterwards formed, and they may therefore be called yolk-granules. At the same time a number of minute siliceous spicules are formed in the cytoplasm, and the majority of the nuclei disintegrate and are absorbed, only about five per cent. of the original number remaining. These remaining nuclei increase in size, and presently the cytoplasm is divided into as many corpuscles as there are nuclei, each corpuscle surrounding itself with a special gelatinous capsule into which the siliceous spicules previously scattered through the cytoplasm are collected. These corpuscles are known as the **primary cysts**. The nucleus of each divides mitotically, and division of the nuclei is followed by the division of each primary cyst into two **secondary cysts** which are destined to become conjugating cells or gametes, and may therefore be described as gametocytes. The mitosis of the nuclei of the primary cysts differs from that already described in the fact that centrosomes are formed from the chromatin of the nuclei. The secondary cysts remain side by side in the pairs in which they were formed, and the nucleus of each divides twice to form two polar bodies. The process may be shortly described as follows:—The nucleus divides mitotically, and one of its halves is expelled from the cyst as the first polar body. The

other half increases in size and again divides mitotically to form the second polar body. Both polar bodies consist only of nuclear material, and speedily disintegrate and disappear. After the extrusion of the polar bodies the secondary cysts have become **gametes** and forthwith proceed to conjugate. The remarkable feature in Actinosphærium is that conjugation is limited to the original pairs formed by the division of the primary cysts. The members of each pair fuse together again, nucleus with nucleus and cytoplasm with cytoplasm, to form **zygotes**, the number of which is, of course, equal to that of the original primary cysts. Each zygote becomes a **spore** with a firm spore-coat of two layers; externally a siliceous envelope formed by the union of the loosely scattered spicules of previous stages, and within this a tough resistant membranous coat. The spores remain in this condition for weeks together, and then on the onset of warmer weather the spore-coats, and also the gelatinous cyst-wall, are ruptured, and from each spore a young Actinosphærium emerges. These young forms are vacuolated and protrude pseudopodia. Each has several nuclei, formed by mitotic division of the single spore nucleus either immediately before or during emergence, but it would appear that before growing any further it divides into as many pieces as there are nuclei, so that the end result of this long and complicated process is a brood of young uninuclear Actinosphæria, which proceed forthwith to feed and grow, the single nucleus dividing to form many as growth proceeds.

CHAPTER VI

THE MYCETOZOA (SLIME-FUNGI)

BADHAMIA UTRICULARIS

In damp woods the trunks of old and decaying trees, especially elm-trees, are often seen to be infested with a greyish-yellow parasitic fungus **Stereum hirsutum** projecting like a shelf from the surface of the bark. Similar fungi may be found on fallen trees, damp decaying timber, old garden seats or arbours, and other such places. A search under the bark or on the surface of such timber will generally reveal the presence of a bright yellow slimy substance spreading over the surface of the wood or beneath the bark. This yellow gelatinous and shapeless mass is the plasmodium of Badhamia, and the Stereum is its food. If a mass of the bright yellow slime be carefully removed, whilst still attached to the wood or to a piece of Stereum, and kept in a dry place, it loses its slimy character, dries up, and forms a thin yellow incrustation which can be chipped off in flakes resembling so much yellow sealing wax. This dry condition of the Mycetozoon is known as the **sclerotium**. The protoplasm is not dead, but has simply passed into a resting or encysted condition, enabling it to withstand prolonged drought. Pieces of the sclerotium of Badhamia which have been kept for as long as three years may be revived by being brought into a moist chamber. Examination shows that the sclerotium is formed of a number of cysts or chambers, separated from one another by firm partition walls, each cyst containing some ten or twenty nuclei. If a piece of sclerotium be soaked in water for about twelve hours and then placed on a moist surface (wet blotting-paper placed under a bell jar serves very well for the purpose) it will gradually revive and pass again into the plasmodium stage. The opaque horny walls of the cysts become soft and semi-transparent, the contours of the fragment become rounded and

irregularly lobed and puckered, and presently it reverts to the slime-like condition, and begins to move, but so slowly that the motion is imperceptible to the eye. In fact, it awakes once more into life. A plasmodium may be of considerable size, covering as much as six square inches, or it may be small, of the size of a sixpence or threepenny bit, but, whether small or large, it shows the same structure. It spreads out over the surface on which it crawls in the form of a network of protoplasm, or rather of a thin sheet of protoplasm traversed by numerous thicker veins of various dimensions which anastomose with one another, and give the whole a reticulate appearance. In some places the veins are not united by the thin sheet of protoplasm, so that the meshes are empty and a true reticulum is formed. The edges of the plasmodium are usually thickened and puckered in an irregular manner, and occasionally processes of protoplasm, pseudopodia, may be seen to be protruded from them.

If a small plasmodium is examined under the microscope, for which purpose it can easily be persuaded to crawl over a glass slip, it is seen to consist of protoplasm, the outermost layer of which is clear and transparent, and may be called the ectosarc. The inner mass is opaque and granular, the veins being especially rich in granules. Amongst the granules may be seen particles of inorganic matter, carbonate of lime, and also a large number of round nuclei, each of which has a nucleolus and an achromatic network to which minute chromatin grains are attached. The plasmodium of Badhamia —or any other Mycetozoon—affords an admirable object for studying the characteristic streaming movements of protoplasm. When watched under the microscope the granules of the endosarc are seen to be in a constant state of movement, streaming first in one direction, then in another. The movement is most active in the veins, and is perfectly rhythmical ; the granules stream steadily in one direction for one or two minutes, then slow down and come to rest, and immediately the flow is reversed and they stream back in the direction whence they came.

The plasmodium has been described as crawling slowly over the surface on which it lives. This creeping movement appears to be associated with the internal flow of protoplasm, for the streaming movements last longest in the direction in which

Fig. 33.

A, a portion of a plasmodium of *Badhamia utricularis*, showing the frilled edge and the reticulated protoplasmic mass. *B*, a small portion of the plasmodium highly magnified, showing the vacuolated protoplasm and the numerous nuclei. *C*, spore fruits of *Badhamia magna*; *sp*, spore cases; *cap*, capillitium. (*C*, after Lister.)

locomotion is taking place. It is easy to observe that this slimy sheet of protoplasm, the plasmodium, is irritable, selective and assimilative. If the surface on which it crawls becomes too dry it will move off to a wetter portion of it. If exposed to a bright light it will move off to any shaded corner which is available; unless, indeed, it is about to form spores, when it will move out of the shade and seek the light; and under the same circumstances it will leave a damp for a drier situation. Still more characteristic are its movements in search of food. If a plasmodium is creeping along one edge of some moist surface—a sheet of wet blotting paper or a piece of wood—and a piece of its food fungus, Stereum, be placed at the opposite edge, the whole plasmodium will move off towards it, flow over it, and engulph it. Small pieces of the fungus or individual hyphæ are soon seen to be ingested, and each ingested piece is enclosed in a food-vacuole which is probably secreted round it, just as in Amœba. The protoplasmic contents of the hyphæ are digested and assimilated, the indigestible remains being expelled much in the same way as in Amœba. These movements in search of moisture, shade, or food are so slow as to be imperceptible; but if a plasmodium, with a piece of its food-fungus placed a few inches away from it, be left for a while, it will be found, after a few hours, to have advanced up to its prey, and to be surrounding it. A plasmodium may be killed in osmic acid, or any other of the ordinary killing and fixing reagents, and stained for examination of the nuclei. These are very numerous, and they continue to multiply, as long as the plasmodium is active and well fed, by mitotic division. In mitosis a spindle of achromatic fibres is formed, the chromatin is gathered at the equator of the spindle in the form of a number of chromosomes, which divide, and their products pass to opposite poles of the spindle in the usual manner. There is some evidence that in an actively-moving and streaming plasmodium the nuclei also multiply amitotically, but actual division of the nucleus without mitosis has not been seen. The reproduction of Badhamia is so similar to that of some of the lowest forms of plants, that it and its allies are described in botanical works as plants. When reproduction is about to take place, the plasmodium emerges from under the bark or crevice of wood in which it may be hidden, and seeks the light. The protoplasm is concentrated and accumulated at

certain points where it may be seen to pulsate in a rhythmic manner. The waves of contraction advance and recede, but gradually the advancing movement predominates, and little prominences are formed, the basal part of each contracting to form a stalk consisting of a tube of a tough hyaline substance through which the protoplasm continues to flow till all the contents of the neighbouring parts of the plasmodium become aggregated on its summit in the form of a spherical mass. The outer layer of this mass hardens and thickens to form a wall surrounding the more fluid contents, and part of the calcareous granules which were scattered through the plasmodium are incorporated into the substance of the wall. The fluid contents become differentiated into two structures. First a part of the protoplasm gives rise to a branching system of flattened threads, spreading like a network from the base of the chamber to its wall. The threads are expanded where they unite together, and contain a number of lime granules evenly distributed through their substance. The whole system of branching threads is called the **capillitium**, and the remaining mass of protoplasm filled with nuclei may conveniently be named the **sporoplasm**. As yet no conjugation of nuclei prior to spore formation has been observed in Badhamia, but in *Arcyria* and some other Mycetozoa the nuclei of the sporoplasm have been observed to fuse together in pairs, forming half as many conjugation nuclei or **synkaryons**. In each synkaryon eight bivalent chromosomes make their appearance and it is supposed, though the evidence is not very clear on this point, that one moiety of each bivalent chromosome is derived from one, the other moiety from the other, of the two conjugating nuclei. A heterotypic or meiotic division then takes place simultaneously in all the synkaryons, as a result of which each is divided into two daughter-nuclei containing eight univalent chromosomes. While the meiotic division is in progress the protoplasm breaks up into a number of lobed masses each containing from six to ten nuclei. Eventually these masses are divided into as many corpuscles as there are nuclei. Each corpuscle containing a single nucleus is a **spore**: it acquires a cell-wall composed of a substance resembling the cutin of cuticularised vegetable cells, and a period of rest ensues. Each globular chamber borne on its stalk is called a **sporangium**. The sporangia of **Badhamia**

utricularis are ovoid or globular, of a grey or iridescent violet colour, clustered and borne on membranous straw-coloured branching stalks. The capillitium is a network of flat bands, with broad thin expansions at the angles, and lime granules evenly distributed through the strands. The spores themselves are from 9 to 12 μ in diameter, of a bright brown colour.

After some time the external wall of the sporangium breaks down, and the spores are exposed hanging on the threads of the capillitium. They are gradually scattered and disseminated, and if kept dry retain their vitality for an almost indefinite time. But if they are wetted the spore coats are ruptured, and their contents emerge as a number of pellucid globules, which lie quiescent for a few minutes and then begin to put forth pseudopodia and exhibit amœboid movements. A few minutes more and each animalcule becomes pear-shaped, develops a contractile vacuole, a single flagellum at its narrow end, and swims off with a dancing movement, the flagellum at the narrow end being in advance, whilst pseudopodial processes are given off from the broad posterior end. These active bodies are known as **flagellulæ**, and they feed actively on living bacteria caught by the pseudopodia at the hinder end. The flagellulæ, if well fed, multiply rapidly by binary division, but after a time they become sluggish in movement, withdraw their flagella, and creep about by their pseudopodia. In this condition they are known as **amœbulæ**. When two amœbulæ come into contact they coalesce, the protoplasm of the two running together, whilst the nuclei remain separate. Other amœbulæ are attracted to the spot, often in great numbers, and after a time the cytoplasm of all becomes confluent, and a new plasmodium is formed. It should be noticed that the union of the amœbulæ to form a plasmodium is not a case of conjugation but of **plastogamy**, for there is no union of nuclei but only of cytoplasm. On the other hand, it is clear that the fusion of the nuclei of the sporoplasm in pairs previous to spore formation in Arcyria is a true process of conjugation. Furthermore, if the somewhat fragmentary accounts of the heterotype mitosis immediately following conjugation are substantiated by further research, the highly interesting fact will be established that in Mycetozoa only half the full number of chromosomes are present in all the numerous nuclear divisions intervening between the amœbula stage and

the conjugation of the nuclei in the sporangia. The full number is restored by conjugation, but is promptly reduced to half by the meiotic division immediately following. In other words, it would seem that in the life cycle of the Mycetozoa all the nuclear divisions but one belong to the so-called postmeiotic phase, and therefore correspond to the two postmeiotic divisions of the spermatocyte described on p. 122.

Badhamia is a member of a large class of organisms which live on decaying organic substances. It alone, in the plasmodial condition, feeds upon living fungi, though the flagellulæ of a large number of species have been observed to feed on living bacteria. Now, the ingestion of solid organic substances and their digestion within the body are essentially animal characteristics, and seem to justify the claim of zoologists to the possession of Badhamia. But many of its allies, such as the common **Fuligo septica**, or "flowers of tan," found in old tan-pits, feed on decaying vegetable matter only, and in this respect rather resemble the Fungi in their mode of nutrition. The whole group of the Mycetozoa is further held to resemble the lower plants, because of the manner in which the sporangia are formed, and because the spores themselves have coats of cutin and sometimes of cellulose, two characteristically vegetable products, though cellulose is not unknown in the animal kingdom. But a discussion as to whether they are animal or vegetable would be fruitless. Organic nature does not lend itself to sharp distinctions and the Mycetozoa, of which our Badhamia is taken as an example, afford one of the best instances of the convergence of the two great types of organic structure, plants and animals, so widely different in their higher forms.

CHAPTER VII

THE SPOROZOA, MONOCYSTIS MAGNA AND MONOCYSTIS AGILIS

The Protozoa described in the previous chapters are free living animals, moving about in search of various kinds of solid food and ingesting it when found. Some few members of the Rhizopoda, it is true, are parasitic and inhabit the alimentary canal of various animals, including man, but they may be considered as exceptional, as they do not exhibit any marked structural modification or specialised mode of reproduction in connection with the parasitic habit. The class **Sporozoa**, on the other hand, consists exclusively of parasitic Protozoa which infest the cavities or tissues of almost every class of vertebrate and invertebrate animals. As is commonly the case with parasitic animals, each species of sporozoon is, as a rule, exclusively confined to some particular species of animal called its **host**, and frequently to some particular organ or tissue of that host. Some infest the internal cavities of the body; others are, at some period of their existence at least, cell-parasites—that is to say, they live inside tissue-cells of their host. But whatever situation they may affect, all Sporozoa are alike in this respect, that they do not ingest solid food, but absorb the juices of their hosts by osmosis through the whole surface of their bodies. They likewise all resemble one another in being able to multiply rapidly by means of **spores**. A spore is a minute reproductive body produced, as a rule, by division of the parent form, and the various kinds of spore-formation in this class afford instructive examples of the adaptation of animals to different modes of existence, for each kind is clearly suited to the dissemination of the spores in such a manner as to ensure their transference from host to host.

The two species, *Monocystis magna* and *Monocystis agilis*, form convenient examples for the study of Sporozoa, because

they can easily be found in almost every individual of the common earthworm. The former is a sporozoon of large size, attaining to a length of 5 mm. and therefore easily visible to the naked eye. The mature individuals are found adhering by one end of their elongated bodies to the rosette-shaped sperm-funnels of the sperm-ducts of the earthworm. The mature form of *M. agilis* is only about ·2 mm. in length and is found in the sperm-sacs of the earthworm, where, as its name implies, it moves actively among the developing spermatozoa of its host. In either case the parasite is a single elongated cell (fig. 34, *D*), consisting of a granular, opaque, central medullary mass or endoplasm, and an external, hyaline denser layer of ectoplasm. External to the ectoplasm is a very thin but distinct membrane or **cuticle**, which in the two species under consideration is covered with very fine longitudinal striations. Careful examination with the microscope shows that the ectoplasm is more highly differentiated than is the case in Amœba. Its deeper layer is modified to form a number of very fine contractile fibres generally known as the **myocyte-fibrillæ**, which run transversely round the body, and are therefore at right angles to the longitudinal striations of the cuticle. These myocyte-fibrillæ give off branches which anastomose with one another, so that the whole forms a network whose meshes are elongated in a direction transverse to the long axis of the body. The presence of a cuticle and the differentiation of a special contractile layer of the ectoplasm together confer a more or less definite shape upon the body. The shape, however, is not constant, for if a lively specimen of Monocystis is kept under observation it will be seen to exhibit regular but sluggish movements, due to the contractility of the myocyte-fibrillæ. A constriction appears at one end of the body and travels slowly to the other end, and as it passes the animal is swollen now at one end, now in the middle and now at the other end, these changes of form being accompanied by more or less pronounced bending movements from side to side. The endoplasm is not contractile and during these changes of form undergoes passive movements such as would be exhibited by the fluid contents of an elastic bag squeezed by passing the hand from one end to the other. As the parasite approaches maturity the endoplasm becomes filled with a number of coarse ovoid granules which give a

colour reaction with sulphuric acid and iodine, and are therefore recognised as belonging to the class of starches. They must be regarded as a store of reserve food material stored up in preparation for impending reproductive processes. The nucleus is lodged in the endoplasm. It is a spherical body, with a distinct nuclear membrane and clear contents. In the latter are several deeply staining bodies, resembling nucleoli, but as each consists of a corpuscle of achromatic plastin with which a certain quantity of chromatin is associated, they are called **karyosomes**, to distinguish them from true nucleoli which consist of plastin only. The Sporozoa are probably degenerate in consequence of their parasitic habit, and accordingly we find that Monocystis has no pseudopodia, no flagella or cilia and no contractile vacuole.

The foregoing description refers only to the full-grown individuals of Monocystis ready to enter upon the reproductive phase of their life history. Previous to this there was a period of inactivity during which the animal absorbed nutriment, grew in size and stored up the granules of reserve material in its endoplasm. In the sub-class Telosporidia, to which Monocystis belongs, this period of purely vegetative growth is sharply marked off from the period of active reproduction that follows: it may therefore conveniently be referred to as the **trophic** phase of existence, and each individual parasite during this phase may be called a **trophozoite.** The earliest known stage of the trophozoite of Monocystis agilis is a minute nucleated corpuscle of protoplasm lodged in one of the mulberry-shaped cell-masses formed by the developing spermatozoa of the earthworm (fig. 34, *B*). The last-named are formed by the repeated divisions of a sperm-mother cell; but instead of the whole of the protoplasm going to form spermatozoa, a central cylinder of residual protoplasm, the **sporophore**, is left, to which the heads of the spermatozoa are attached. It is in this sporophore that the young trophozoite lives and, absorbing its contents, grows up into the mature form. The development of the spermatozoa proceeds, in spite of the presence of the parasite, and the latter eventually appears to be clothed by a coat of long cilia, which are, in fact, the tails of the spermatozoa, now withering for want of nutriment. The young trophozoite is therefore a cell-parasite and only quits its cell-host to wander free in the

sperm-sac when it has absorbed all the available nourishment.

In the reproductive phase of the life cycle, which is practically identical in the two species under consideration, three distinct events may be recognised. Firstly, there is the associa-

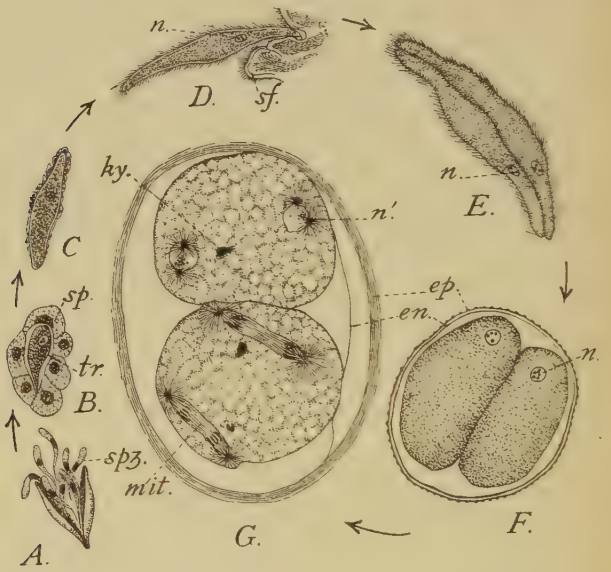

Fig. 34.

A, the eight sporozoites, *spz*, of Monocystis escaping from the Sporocyst. *B*, a young trophozoite lodged in the centre of a sperm-morula of the earthworm; *tr*, trophozoite; *sp*, sperm-mother cells. *C*, a free individual of *M. agilis*, with a few withered sperm cells adhering to it. *D*, a mature individual of *M. magna* attached to *sf*, the sperm funnel of an earthworm. *E*, two mature individuals of *M. magna* joined in "association." *F*, the two associates have become hemispherical and have formed a cyst; *ep*, epicyst; *en*, endocyst. *G*, a section through two encysted associates showing nuclear division in progress; *ky*, a degenerating karyosome; *mit*, a much elongated mitotic spindle of a dividing nucleus; *n'*, resting nucleus preparing for division. (*A-C*, original; *D-G* after Cuénot. *A* is purely schematic, the liberation of the sporozoites not having been actually observed in *Monocystis*.)

tion and enclosure in a common cyst-wall of two mature trophozoites, a process which must by no means be confounded with conjugation. Secondly, there is the subdivision of the

bodies of the two associates into a number of minute nucleated corpuscles or gametes, which conjugate in pairs. Thirdly, there is the formation of resistant spores by whose means the parasite is disseminated and introduced into new hosts. The course of these events is as follows. Two mature trophozoites which as they are destined to give rise to gametes may now conveniently be called **gametocytes**, come together in close apposition (fig. 34, *E* and *F*). While retaining their individuality, they lose their characteristic form, become hemispherical, and together form a subspherical mass, which undergoes slow rotatory movements while secreting a cyst-wall from its surface. First an outer rigid **epicyst** is formed, afterwards an inner thin and soft **endocyst**. During the formation of the cyst the two associated gametocytes shrink in size and a space filled with fluid is formed between them and the cyst-wall, but although enclosed in a common envelope, they are still perfectly distinct from one another and separated by their cuticles at the surface of contact. While the cyst is being formed the nucleus of each gametocyte undergoes changes preparatory to division. The karyosomes diminish in volume and are partly dissolved in the nuclear sap, while in their place small granules or short filaments of chromatin make their appearance. A centrosphere with astral rays appears outside the nucleus; the nuclear membrane disappears and a mitotic spindle is formed which elongates until it stretches right across the body of the gametocyte (fig. 34, *G*). The two daughter-nuclei resulting from the division are smaller than the parent nucleus and situated at opposite ends of the body. They divide again with mitosis to form four grand-daughter nuclei of smaller size, and the process is separated again and again. At each division the nuclei reform, rest awhile, and then undergo a fresh mitotic division. Eventually a large number of minute nuclei are formed, mostly collected near the periphery of each gametocyte. Throughout this period the two associated individuals have retained their identity, but now the cytoplasm of each divides into several irregular fragments each containing a number of nuclei projecting from its surface. The nuclei then become surrounded by clear protoplasm, which is presently segmented into a number of small ovoid cells, each containing a single nucleus and attached by its base to the residuum (fig. 35, *A*). The minute nucleated cells thus

formed used to be known as sporoblasts, but now that their nature is more fully understood they are more appropriately

Fig. 35.

A, part of a section through a gametocyte showing the gametes, *gam*, formed at the periphery of a mass of residual protoplasm, *rp*; *rn*, an abortive nucleus in the residual protoplasm. *B*, conjugation of the gametes in pairs to form zygotes; in *zy* the nuclear fusion is complete; *en*, endocyst; *ep*, epicyst; *rp*, residual protoplasm containing paraglycogen granules. *C*, the zygotes have begun to secrete spore coats or sporocysts, and each is now a definitive sporoblast, *sp*. *D*, a single sporoblast in which eight nuclei have been formed by successive divisions of the conjugation nucleus. *E*, a transverse section through the equator of a fully developed sporocyst showing the nuclei of eight sporozoites surrounding a core of residual protoplasm, *rp*. *F*, a fully developed sporocyst (pseudonavicella) containing eight sporozoites, *spz*. (*A-C* after Cuénot; *D-F* original.)

termed **gametes**. They soon become detached and float in the cystic fluid near the periphery of the cyst. The centre of the cyst is occupied by a granular mass of residual protoplasm,

containing paraglycogen granules and a few abortive nuclei, and there is no longer any trace of the individual gametocytes.

The gametes now begin to move actively in the cystic fluid; how their movements are affected is not accurately known, but after a time they become slower, and then the gametes unite together in pairs and conjugate (fig. 35, *B*). First the cell bodies of each pair fuse together, then their nuclei; but the latter do not form a mitotic figure and the chromatin granules derived from the two gametes do not fuse, but are simply mingled together in the conjugation nucleus. It is not certain, but is very probable, that the gametes derived from one of the associated gametocytes conjugate with those derived from the other gametocyte, and this view is strengthened by the fact that in an allied gregarine, *Lankesteria ascidiæ* parasitic in the alimentary canal of the sea-squirt *Ciona intestinalis*, a similar association of two gametocytes and production of gametes has been observed. In one instance one of the gametocytes perished within the cyst, while the other proceeded on its normal course of development and gave rise to a crop of gametes, but these exhibited no affinity for one another, did not conjugate, and eventually perished for want of partners derived from another individual. The individuals formed by the conjugation are the definitive sporoblasts or **zygotes**: they are of course half as many in number, but each of them is nearly twice as big as the original gametes. They are then, while still contained in the cyst, transformed into spores in the following manner. Each zygote becomes oval in shape and secretes a substance resembling chitin from its surface, which hardens to form a characteristic lemon-shaped spore coat or **sporocyst** (fig. 35, *C* and *D*). Within this protective coat the nucleus of the zygote undergoes three successive amitotic divisions, giving rise to eight nuclei, arranged more or less in the plane of the equator of the spore. A portion of the protoplasm of the zygote is then segmented off round each nucleus, and thus eight minute curved bodies are produced, arranged round a core of residual protoplasm, much as the divisions of an orange are arranged round its central fibrous axis (fig. 35, *F*). During the formation of the spores the cystic residuum is slowly absorbed, and the spherical cyst originally formed by the associated gametocytes contains nothing but a great number of spores which, from their resemblance to the

boat-shaped diatoms of the same name, have long been known to naturalists as **pseudonavicellæ**.

The eight minute nucleated bodies contained in each spore were formerly called the falciform (*i.e.* sickle-shaped) young but are now known as the **sporozoites**. Protected by the tough and impervious sporocyst they are incapable of further development until transferred to the body of another earthworm, but are in a condition to withstand such adverse influences as they may encounter during the transference. Their actual history at this stage has not yet been traced. It seems certain that the spores are by some means scattered broadcast in the earth and are swallowed by another earthworm, the action of whose digestive juices causes the sporocyst to split open and set free the contained sporozoites. The sporozoites are not only active but have the power of boring their way through the walls of the gut and other tissues of their new host till they reach the reproductive organs, where they penetrate into the sperm-mother cells, become quiescent, and enter upon the trophic phase of existence. But the manner in which the spores are scattered in the earth is not accurately known. There is no evidence that they are passed to the exterior through the sperm-ducts. It has been suggested, and the analogy of other Sporozoa whose life histories are better known affords good grounds for the suggestion, that they are disseminated by the agency of worm-eating birds. The protective sporocyst would enable the spores to pass uninjured through the alimentary tract of a bird and pass out with the fæces, whence they would be washed down into the soil and readily swallowed by other earthworms. However this may be, the transference of the spores from one host to another remains a problem which still awaits experimental solution.

A consideration of the foregoing description will show that the life history of the common species of Monocystis of the earthworm is really a simple one. Much of the apparent complexity is due to the fact that different names are used to indicate the different stages of growth of one and the same individual. Thus sporozoite, trophozoite, gametocyte, are names used to designate successive stages of growth of a single individual and though they may be confusing at first because of their novelty, when once they are understood they should no more embarrass the reader than such familiar names

as baby, child, youth and adult, used in common language to designate the different stages of growth of human beings. When two gametocytes become associated in a single cyst they do not lose their identity ; they are only two grown-up parent forms which are keeping company while the reproductive cells that will give rise to a new generation are being formed and matured. The production of gametes from each of the two parent forms or gametocytes is analogous to the production of ova and spermatozoa from multicellular animals, the difference being that in our parasitic protozoon the greater part of the parent body is used up in the formation of the reproductive cells. What remains is simply a granular residuum, serving at the most as nutritive material for the developing progeny. The conjugation of the gametes is clearly an analogous process to the fertilisation of the ovum by the spermatozoon in higher animals. But in Monocystis there is no visible differentiation of sex; the two conjugating gametes are so much alike that it is impossible to say that one is male and the other female. The parasite is therefore called **isogamous.*** The zygote resulting from conjugation is clearly the equivalent of a fertilised ovum which as a result of developmental processes will grow into a new organism like its parent. It is at this stage that the special features of sporozoon development come into prominence. The zygote does not grow at once and directly into the adult form. It begins by surrounding itself with an impervious envelope, this being an adaptive structure serving as a protection against destructive influences during its transference from the old host to a new. Moreover the zygote multiplies itself asexually within its protective coat. The eight sporozoites formed by division of the sporoplasm represent a new cell generation, whose obvious utility is to

* Since this chapter was written R. Hofmann (Ueber Fortpflanzungserscheinungen von Monocystideen des *Lumbricus agricola*, Archiv f. Protistenkunde XIII., December 1908) has described anisogamy in a species of Monocystis infesting one of the common earthworms. Of the two associated gametocytes one produces gametes of the ordinary form ; the other gives rise to gametes shaped like indian clubs, the nucleus being situated at the junction of the handle with the body of the club. The act of conjugation was not observed, but it is presumed that the indian-club shaped forms are male or **microgametes** and that each conjugates with an oval female form or **macrogamete**. Thus, in one species of Monocystis, at least, the gametes are of two kinds, but it appears that other species are isogamous as described above.

ensure the perpetuation of the species, for however numerous the gregarines contained in a single earthworm, and however numerous the spores produced by them, the chances of any given spore surviving to be swallowed by another host of the right species are, to say the least of it, precarious. Thus, though it is usual to describe the life cycle of Monocystis as **monogenetic**—*i.e.* as consisting of a single cell generation—a more careful analysis shows that it is in fact **digenetic**. There is clearly an alternation of a sexual generation—the gametocytes—with a generation that multiplies itself asexually—the zygote or sporoplasm. It is the offspring of this second generation that grows up into the sexual form. There are, however, some gregarines in which the zygote does not multiply within the sporocyst, but simply becomes a single sporozoite. Such forms are truly monogenetic. But attention must be directed to the fact that the sporozoite of Monocystis, when once it has found a lodgment in the locality appropriate to it, leads a purely vegetative existence and grows up into the gametocyte without multiplying itself asexually and causing re-infection of other tissue cells of its host. Since only a limited number of cells are attacked at one time Monocystis and its allies are harmless parasites and do not cause the death of or even seriously inconvenience the animals they infest. The various members of the order Gregarinida, of which Monocystis is an example, are parasitic in all kinds of invertebrate animals, but not in vertebrates. They are mostly innocuous, and with the rarest exceptions the whole life cycle of any given species is completed within a single host. The resistant spores produced by them are adapted for dissemination and the casual infection of new hosts. The spores either pass out of the host's body by natural channels, and are scattered about to be swallowed accidentally by another animal of the same species, or if swallowed by an animal of a different species they pass unaltered through its digestive tract and do not undergo any developmental changes within it. In this case the second animal is only an agent in dissemination, is not itself infected, and does not serve as a carrier of infection. But many other Sporozoa, particularly those infesting vertebrate animals, have a most pernicious effect upon their hosts. The trophozoites in such cases multiply very rapidly by division and their numerous offspring

infect whole tracts of tissue cells, causing serious illness and even the death of the infected animal. In some Sporozoa, also, one portion of the life cycle of the parasite is passed in one host, and the other portion in another host of a quite different kind, this second or intermediate host serving as a carrier of infection from one primary host to another. In such cases considerable complications are introduced into the life cycle, as will be explained more fully in the next chapter.

CHAPTER VIII

THE MALARIAL PARASITE

PLASMODIUM (v. HÆMAMŒBA) MALARIÆ, VIAVX, AND IMMACULATUM

Of the various ills that mankind is subject to, none is more widespread or more destructive than the fever known as malaria, ague or marsh-fever. It probably takes a higher toll of human life than any other disease. In India it has been estimated that 40 per centum of the annual death rate is due to various kinds of malarial fever, which therefore claims six times as many victims as cholera. Malaria has destroyed armies, as in the case of the ill-fated Walcheren expedition in 1809,* has ruined cities and depopulated large tracts of country. A disease so disastrous has naturally engaged the attention of the medical profession from the earliest times, and even among the ancient Romans various theories were current to account for its causation and dissemination. But it was only in 1882 that A. Laveran, a medical officer in the French army, discovered the true cause of the disease in a sporozoon parasite infesting the red blood corpuscles, and scarcely a decade has elapsed since the whole life history of the parasite has been worked out. Malaria occurs in tropical and temperate climates all over the world, with the exception of some oceanic islands, but is not known in high northern and southern latitudes. It was formerly endemic in certain parts of England, especially in the Fens and in the low-lying country bordering on the

* From the 28th August to the 23rd of December, out of an effective strength of 39,219 men, 4175 succumbed to fever. From the 21st of August to the 18th of November the number of admissions to the hospitals, including recurrent cases, rose to 26,846. Towards the end of December 1809, after the return of the troops to England, 11,503 men were still reckoned as suffering from "Walcheren sickness." The English army had been vanquished before it had joined combat; only 217 men had been killed by the enemy (A. Laveran, Traité de Paludisme, Paris, 1898).

estuary of the Thames, and extended into Scotland and Ireland, but now it has happily disappeared. Malaria is essentially a disease of marshy and low-lying districts. It is most prevalent near the mouths of rivers, in places liable to inundations, where pools and lagoons of stagnant water are left by the receding waters, or where the subsoil is wet. In all latitudes its intensity diminishes in hilly country and at high altitudes it disappears altogether. It is most prevalent in the summer and autumn months. For a long time it was supposed that poisonous emanations from the soil were the cause of malaria, and hence the name *mal'aria*—bad air. Afterwards when micro-organisms of different kinds came to be recognised as disease-producing agents, malaria was variously attributed to bacterial or fungal spores borne in the air or conveyed into the system by impure drinking water. But even in remote times sundry observers had noted that violent malarial epidemics were coincident with the appearance of unusually large numbers of winged insects, and it is now proved beyond all doubt that the parasite is disseminated by mosquitoes of the genus *Anopheles*. Mosquitoes may occur in districts where there is no malaria, but malaria never occurs in districts where there are no mosquitoes.

As will appear in the sequel, the sporozoon which causes malarial fever is as truly parasitic in the mosquito as in the human subject, with this difference: that whereas it produces pernicious and even fatal effects in the latter, it appears to be innocuous to the former. As an introduction to the detailed account that will follow, it may be stated here that the life history of the malarial parasite comprises an asexual cycle and a sexual cycle. The asexual cycle is passed through in human blood, and is characterised by the rapid multiplication by division of the trophozoite, resulting in the continuous or recurrent infection of vast numbers of red blood corpuscles. The sexual cycle is passed through in the body of an Anopheles mosquito, which has sucked the blood of an infected human subject. Thus, for the completion of the whole life cycle of the parasite, two hosts are necessary, a principal and an intermediate. Without prejudice to the theoretical views on the subject, it will be convenient to consider man as the principal and the mosquito as the intermediate host.

The name "mosquito," which is the diminutive of *mosca*,

a fly, is a popular one, and in common language is loosely applied to all sorts of insects belonging to the family Culicidæ, and even to other families. As a rule where Culicidæ are very abundant and pertinacious they are called mosquitoes;

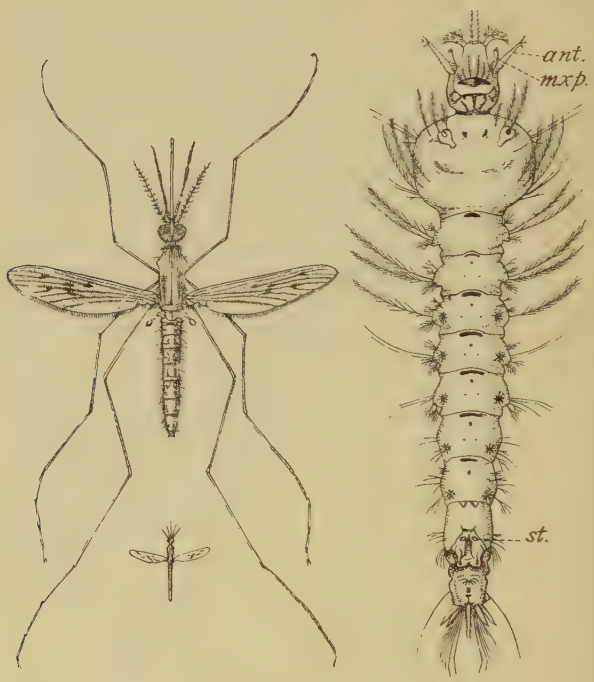

Fig. 36.

On the left hand a figure of a "dapple-winged" mosquito, *Anopheles maculipennis*, ♀; the small figure below indicates the natural size of the animal. On the right hand a fully-grown specimen of the aquatic larva of the same species, about eight times the natural size. *Ant*, antennæ; *mxp*, maxillary palp; *st*, stigmatic opening of the respiratory organs of the larvæ. (After Nuttall and Shipley.)

where less troublesome they are called gnats. The true mosquitoes and gnats are dipterous insects of the family Culicidæ. They have small heads with large eyes; slender bodies and legs; a single pair of narrow wings; and long

thirteen-jointed antennæ bearing whorls of bristles, which are specially long in the male, giving the antennæ a feathery appearance. These features are shared by some other closely allied dipterous insects, but Culicidæ are characterised by two features; they have a long suctorial proboscis, and the veins and lower margins of the wings are covered with minute scales. They lay their eggs in the water and the larvæ hatched out from the eggs are aquatic and incapable of sustaining life if placed in the dry. Hence the stories which from time to time appear in newspapers attributing unusual swarms of mosquitoes in hotels to the introduction of eggs and larvæ in the luggage of visitors arriving from tropical countries are mere fables, founded on a complete ignorance of the natural history of the insects. The most common culicid in Great Britain is the so-called grey gnat, *Culex pipiens*, a species which is also widely distributed in other countries. The female of *C. pipiens*—for it is only female gnats and mosquitoes that suck blood—is as pertinacious a blood-sucker as any mosquito, but does not serve as the intermediate host of the parasite of human malaria. It is an interesting fact, however, that birds suffer from a form of malaria analogous to that of man, and similarly caused by a sporozoon parasite infesting the red blood corpuscles. *Culex pipiens* is the intermediate host of avian malaria, but is impervious to human malaria. On the other hand *Anopheles*, to which the name mosquito may conveniently be restricted, is impervious to avian, but is the intermediate host in human malaria.

To understand the manner in which Anopheles introduces the malarial parasite into the blood, it is necessary to know something about the structure of the proboscis and its action in blood-sucking. Only the female proboscis will be described, the mouth parts of the male being incapable of perforating the skin.

The mouth parts of an undifferentiated insect such as a cockroach or grasshopper consist of the following parts:—(1) A median unpaired upper lip or **labrum**. (2) A median internal membranous lobe known as the tongue, lingula or **hypopharynx**. (3) A pair of chitinous biting jaws, the **mandibles**. (4) A pair of **maxillæ**, consisting of two basal joints, of which the second bears on its inner side two biting lobes and on its outer side a jointed tactile appendage or

palp. (5) A lower lip or **labium**, which is really the second pair of maxillæ whose component parts are fused together in the middle line.

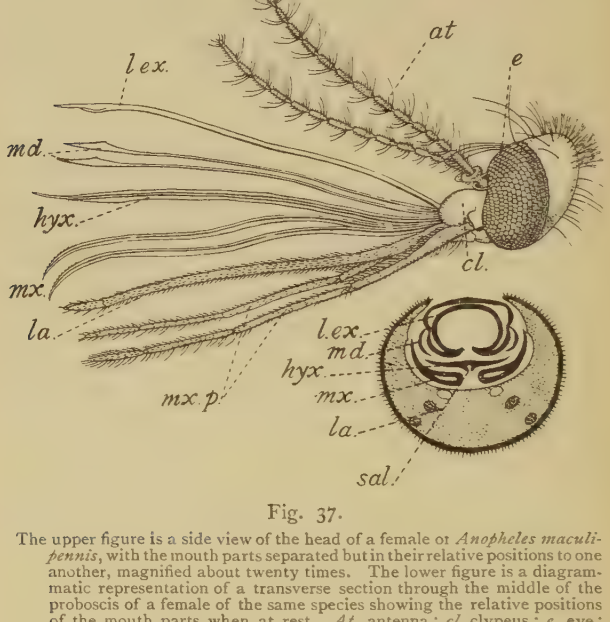

Fig. 37.

The upper figure is a side view of the head of a female of *Anopheles maculipennis*, with the mouth parts separated but in their relative positions to one another, magnified about twenty times. The lower figure is a diagrammatic representation of a transverse section through the middle of the proboscis of a female of the same species showing the relative positions of the mouth parts when at rest. *At*, antenna; *cl*, clypeus; *e*, eye; *hyx*, the sword-shaped hypopharynx; *la*, labium; *l.ex*, labrum+epipharynx; *md*, mandibles; *mx*, maxillæ; *mx.p*, maxillary palps; *sal*, groove-shaped duct of the salivary gland running in the mid-rib of the hypopharynx. (After Nuttall and Shipley.)

The so-called proboscis of the mosquito is formed by the modification and adaptation of these mouth organs. The labium is converted into a long fleshy half-tube, whose extremity is divided into two lobes. In section the labium is crescentic, with the concavity of the crescent directed upwards. It serves as a sheath for the guidance and protection of six piercing organs or stylets, formed by the modification of the remaining mouth parts of a typical insect. Of these stylets one, formed by the fusion of the labrum with an

internal piece called the epipharynx, is median and dorsal in position. One, the hypopharynx, is median and ventral in position. Two pairs, corresponding to the mandibles and maxillæ, are lateral. The labrum + epipharynx lies, when the mouth parts are at rest, between the lips of the groove of the labium; it has the form of a nearly complete tube with a fissure extending along its ventral surface and its extremity is produced into a sharp point. The ventral fissure of the labrum and epipharynx is closed below by the hypopharynx, which is a long flat chitinous blade, in shape resembling a two-edged sword, and ending in a very sharp point. A distinct thickened ridge, channelled by a deep groove leading into the duct of the salivary gland, runs like a mid-rib down the centre of the blade, and the salivary groove is continued down to the extreme point of the latter. The mandibles have the form of a pair of very fine chitinous rods ending in somewhat expanded lancet-shaped extremities, with very finely serrated upper edges. The male Anopheles has no mandibles. The maxillæ are somewhat broader chitinous blades with decurved pointed and serrated extremities. From the bases of the maxillæ spring the soft four-jointed maxillary palps, which are tactile in function and not used in sucking blood.

The female Anopheles, when she settles on the skin and prepares to draw blood, moves her antennæ and labial palps upwards out of the way of the proboscis. She feels about with the bilobed extremity of the labium, and having found a suitable spot pierces the skin by working the stylets to and fro. The six stylets are then thrust deeply into the puncture, and saliva is injected through the aperture in the hypopharynx. The saliva contains a poisonous substance causing the tissues adjacent to the wound to itch and swell: probably this substance prevents the blood from clotting as it is sucked up by the mosquito. The blood passes through the tube formed by the labrum + epipharynx in front and the hypopharynx behind into the mouth. The labium does not penetrate the wound but rests on the surface at the point where the stylets were thrust in and serves to direct and steady them. The whole operation takes from two to three and a half minutes.

The sporozoites of the malarial parasite accumulate, in a manner which will be described presently, in the salivary glands of the mosquito, and a number of them are injected

with the saliva into the wound when the insect sucks blood. On entering the blood vessels they at once attack and make their way into the red blood corpuscles, just as the sporozoite of Monocystis attacks and enters the sperm-mother cell of an earthworm.

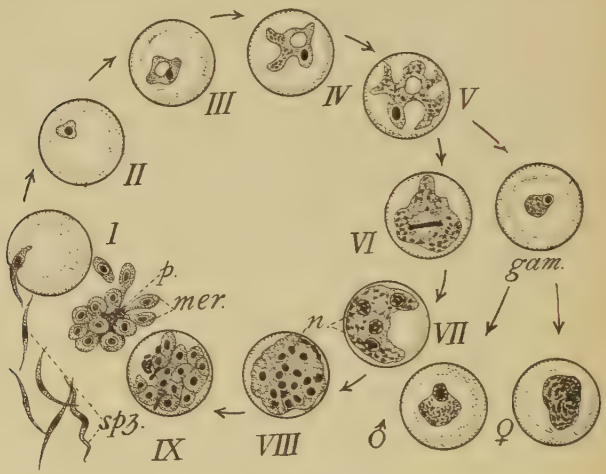

Fig. 38.

A diagram illustrating the stages of the life cycle of *Plasmodium vivax* found in human blood. *I-IX* show the schizogonous cycle. In *I* a sporozoite is boring its way into a red corpuscle; *II*, young amœboid phase; *III*, a vacuole has appeared near the nucleus giving the characteristic ring form; *IV* and *V*, pigment (melanin) granules are deposited in the cytoplasm, the parasite has increased in size and exhibits active pseudopodial movements; *VI*, nucleus with an equatorial ring of chromatin granules; *VII* and *VIII*, successive stages of nuclear division; *IX*, segmentation of the cytoplasm round the nuclei to form the merozoites which are shown at *mer* escaping into the blood plasma. *spz*, sporozoites; *p*, pigment granules; *gam*, a young gametocyte; ♂, a male gametocyte (microgametocyte) and ♀ a female gametocyte (macrogametocyte) of *P. vivax*. In this species and in *P. malariæ* the gametocytes are not crescent-shaped as they are in *P. immaculatum*. (Somewhat diagrammatic after Schaudinn.)

Each sporozoite is a minute spindle-shaped cell, pointed at both ends with a nucleus in the middle of its body (fig. 38, *spz*). It has been observed, in a drop of blood kept under suitable conditions of warmth and moisture under the microscope, to move actively among the corpuscles either by wave-

like contractions of its body, or by wriggling forward by spiral undulations, or by a gliding movement. Under the same conditions it has been seen to penetrate a red blood corpuscle by one of its pointed ends and to gradually work its way in, the whole process lasting about forty minutes. When it has entered the corpuscle the sporozoite assumes a rounded shape and becomes a trophozoite. It soon exhibits active amœboid movements and grows in size at the expense of the substance of the corpuscle. A characteristic feature of its earlier stages is the appearance in the neighbourhood of the nucleus of a large vacuole, which, as it looks transparent in comparison with the surrounding cytoplasm, gives the parasite the shape of a ring (fig. 38, *III*). It is probable that this vacuole is in some way connected with the nutritive processes.

The young trophozoite is unpigmented, but as it grows, granules of a dark brown pigment termed **melanin** are deposited in its cytoplasm. The amœboid movements gradually become slower and finally cease, and the trophozoite when it has attained its full size nearly fills the blood corpuscle. Thus far its growth has been purely vegetative, but it now proceeds to multiply by division, a process which in these forms is known as **schizogony**, and the individual ready to enter upon division is called a **schizont**. The nucleus divides, apparently by a primitive form of mitosis (fig. 38, *VI*), and the two nuclei so formed divide again and again till some dozen or sixteen nuclei are present. The melanin granules become aggregated in the centre of the cell-body, and the cytoplasm then segments into as many corpuscles as there are nuclei, a small amount of residual protoplasm containing the melanin granules being left in the centre. In this manner a number of reproductive bodies named **merozoites** are formed. They escape from the remains of the blood corpuscle into the plasma, and at once attack and make their way into fresh corpuscles, boring their way into them in the same manner as did the sporozoite. On obtaining an entrance they become trophozoites, go through the same phases of growth and division as those just described, and in due time give rise to a new crop of merozoites, which in their turn infect fresh blood corpuscles.

At least three kinds of malarial fever are recognised by the medical profession, the tertian and quartan agues, and the

æstivo-autumnal or tropical malaria. The two first are comparatively mild in their effects, and are known as "benign" intermittent fevers; the third is a pernicious and generally continuous fever. In each case the acute feverish symptoms coincide with the termination of the schizogonous cycle of the life history of the parasite, when the merozoites are set free in the blood and are attacking numbers of previously healthy corpuscles. The three different kinds of fever are attributable to three different species of parasite belonging to the genus **Plasmodium** (also named **Hæmamœba**). The parasite causing tertian ague is **Plasmodium vivax**: in this species the schizogonous cycle is completed in forty-eight hours, and the fever recurs every other day. The parasite of quartan ague is **Plasmodium malariæ**: in this species the schizogony takes seventy-two hours, and consequently the fever recurs once every three days. In **Plasmodium immaculatum**, the parasite of pernicious tropical malaria, the period occupied by schizogony is irregular, and as merozoites are constantly being discharged into the blood the fever is either continuous or recurs at irregular intervals.

From what precedes it is obvious that the number of infected red blood corpuscles in a malarial patient increases in geometrical progression, and more rapidly in the case of tropical than in the benign forms of fever. After a certain number of schizogonous cycles a vast number of red blood corpuscles are destroyed, the patient becomes anæmic; melanin pigment is deposited in the spleen, liver, kidneys, and capillaries of the brain; the spleen becomes swollen and congested, and a condition of general cachexia is produced which may terminate fatally. If the process of asexual multiplication were to continue indefinitely, a fatal result would be certain, and this would be as destructive to the parasite as to its host. But, probably as the result of changes in the blood consequent on the destruction of a large number of red corpuscles, in due time the perpetuation of the parasite is provided for by the production of a number of sexual forms called **gametocytes**. These sexual forms are of two kinds; male forms, known as **microgametocytes**, and female forms known as **macrogametocytes**. Both are developed from the younger forms of the trophozoites, and are generally, though not always, very clearly distinguishable from one another by the distribution of the

melanin granules in the cytoplasm. In the microgametocyte the granules are generally more evenly distributed; in the macrogametocyte they are aggregated round the nucleus. In *P. vivax* and *P. malariæ* the gametocytes are rounded in shape (fig. 38, ♂ and ♀) and are not very easily distinguished from the younger stages of the trophozoite, but in *P. immaculatum* they are readily recognisable because they assume a crescentic form, the convexity of the crescent being closely applied to one side of the corpuscle (fig. 39, *A* ♂ and ♀). Though gametocytes are found in large numbers in the peripheral circulation of malarial patients and can easily be obtained by drawing blood from a finger, they are incapable of further development in the human system, and if they are not transferred to the intermediate host they eventually perish. But if the patient is bitten by a mosquito of the genus Anopheles all stages of the parasite, ring-shaped, amœboid, schizonts and crescents, are drawn up with the blood into the stomach of the insect, and it is a noteworthy fact that all are promptly digested except the gametocytes. These last are not only resistant to the action of the digestive juices, but appear to be stimulated to further development.

The macrogametocyte does not alter much. If it is a crescent form of pernicious malaria, it frees itself from the remnants of the corpuscle in which it was enclosed, assumes a rounded form, and its nucleus divides into two unequal portions. The smaller portion, surrounded by a small investment of cytoplasm, is extruded as a polar body (fig. 39, *B* and *C*), and when this process is completed the macrogametocyte has become a **macrogamete**, ready for fertilisation.

The development of the microgametocyte is more complicated. It becomes spherical and its previously round nucleus assumes an oval shape. At first it is motionless, but suddenly it contracts and the cytoplasm and melanin granules contained in it execute rapid streaming movements. After a few seconds pseudopodial processes are thrust out from various points of the surface, to be withdrawn again and reappear in another place. At this time some of the melanin granules are often cast out of the body. The pseudopodial movements cease for a few seconds and then suddenly some four to eight, most usually six, long slender hyaline processes are thrust out from as many points of the surface, and as soon

Fig. 39.

Figures illustrating the stages of the life cycle of the malarial parasite found in Anopheles. *A*, crescent-shaped gametocytes of *Plasmodium immaculatum* of pernicious tropical malaria; ♂ the microgametocyte; ♀ the macrogametocyte. *B*, further stages in the development of ♂ the microgametocyte and ♀ the macrogametocyte of *Plasmodium vivax*; the nucleus of the macrogametocyte has divided unequally to form a polar body, *pb*. *C*, the nucleus of the microgametocyte has broken up into eight karyosomes, *ky*, each surrounded by a ring of chromatin granules; the polar body has separated from the macrogametocyte. *D*, formation of microgametes from the microgametocyte. *E*, a single microgamete; *ky*, the central karyosome. *F*, fertilisation of the macrogamete by the microgamete; *n* ♂, male pronucleus; *n* ♀, female pronucleus. *G*, the motile zygote or oökinete; *cn*, fertilisation nucleus. *H*, the oökinete (oöcyst) surrounded by a very delicate cyst wall, at rest in the tissues of the wall of the stomach of the mosquito; *n*, nucleus; *p*, pigment. *J*, multiplication of nuclei in the oöcyst. *K*, the protoplasm of the oöcyst has divided into numerous sporoblasts, *sp. bl*, each containing a nucleus. *L*, early formation of sporozoites from the sporoblasts. *M*, a ripe oöcyst full of minute sporozoites, *spz*, which are escaping by the bursting of the cyst; *rp*, residual protoplasm containing an abortive nucleus (*B-G* after Schaudinn, the remaining figures after Grassi. The figures are not all drawn to the same scale.)

as they are formed begin to execute vigorous lashing movements (fig. 39, *D*). At the same time the body of the microgametocyte contracts till it is scarcely more than half its original diameter. While these changes are in progress the nucleus has broken up into eight pyriform or oval masses surrounded by fine granules of chromatin. The pyriform masses are composed of plastin containing a certain amount of chromatin, and are therefore **karyosomes**. At first they lie among the melanin granules in the centre of the cytoplasm (fig. 39, *C*) but soon travel to the periphery of the gametocyte, and a single karyosome with a number of surrounding chromatin granules enters each of the long hyaline protoplasmic processes. The last named are then set free as active filiform **microgametes**, which wriggle away actively in all directions. In each microgamete the karyosome occupies the centre and the chromatin granules are strung out along the length of the rest of the body (fig. 39, *E*). The remainder of the microgametocyte, containing the whole of the pigment granules, is left behind as residual protoplasm and gradually disintegrates. As the number of karyosomes is usually greater than the number of microgametes formed, some of the former are left behind in the residual protoplasm. The next step is the fertilisation of the macrogamete by the microgamete. The former puts forth a conical process of protoplasm, or "cone of reception," from that part of the surface nearest to the nucleus, and as soon as a microgamete touches this cone it adheres to it by one of its extremities and is very rapidly absorbed into it, till only about half of its length remains outside, still continuing to perform lashing movements (fig. 39, *F*). After a short time the whole body of the microgamete is drawn into the macrogamete, and its entry is accompanied by violent streaming movements of the cytoplasm, which slow down and cease in about ten minutes' time, when the female nucleus is found to be situated in the centre with the male nucleus fitted against one side of it like a cap. The two nuclei remain distinct from one another for some little time, but eventually fuse together to form a single fertilisation nucleus or **synkaryon**. The single cell formed by the union of the micro- and the macrogamete is of course a **zygote**, comparable in all essential respects with the zygote formed by the union of two gametes in Monocystis. In the malarial parasite the zygote elongates, assumes a

vermiform shape, and moves actively through the blood contained in the mosquito's stomach. It is because of its activity that it is frequently referred to as the **oökinete**, but it should be borne in mind that the latter name signifies nothing more than that the zygote exhibits a special adaptation to the particular conditions under which it is formed. It has to escape from the digestive cavity of the mosquito and take up a position favourable to its future development. It accordingly bores its way through the epithelial wall of the stomach, comes to rest in the sub-epithelial tissues, again assumes a subspherical shape, a thin and delicate cyst wall is formed around it, and it passes into the stage known as the **oöcyst**. In this condition it is truly parasitic on the mosquito —that is to say, it absorbs nutriment from the juices of its host, and grows so considerably in size that the oöcysts—for they may be numerous—form a number of nodules projecting from the wall of the stomach into the surrounding cavities of the body. As an oöcyst grows its nucleus divides again and again and eventually the cytoplasm divides into as many masses as there are nuclei, the masses not being quite separate, but connected with one another by radiating strands of protoplasm (fig. 39, *J* and *K*). As is so commonly the case, the whole of the protoplasm is not used up in this way, but a certain amount is left over as an anucleate mass of residual protoplasm containing all the melanin granules. Each nucleated protoplasmic mass is comparable with a sporoblast of Monocystis, and may be called by the same name.

The sporoblasts now proceed to form **sporozoites**. In each the nucleus divides repeatedly to form a number of small nuclei, which travel to the periphery of the sporoblast. The surface of the cytoplasm grows out into a number of slender processes (fig. 39, *L*), each of which takes a nucleus with it, and thus a large number of elongate, slender, fusiform sporozoites are formed, radiating outwards from a central mass of residual protoplasm, which is of course the remnant of the body of the sporoblast (fig. 39, *M*). This mass of residual protoplasm may contain one or more abortive nuclei.

The formation of the sporozoites occupies some ten to twelve days, during which time the oöcyst increases greatly in size. Finally it bursts, and the sporozoites are set free

into the blood cavities of the mosquito. They travel along in the blood stream, and by some means not fully understood are collected in the salivary glands, whose secreting cells they penetrate. Hence when an infected mosquito sucks blood and, as described above, injects a drop of saliva into the wound made by its proboscis, it discharges a swarm of sporozoites into the capillaries of the individual whom it has attacked. Each sporozoite promptly attacks and penetrates a red blood corpuscle and forms the starting point for a cycle of schizogonous generations. With the infection of the human blood corpuscle the life history of the parasite is brought round to the point at which it began.

It is a remarkable instance of the close adjustment of parasitic organisms to a strictly limited set of life conditions that, if a human malarial patient is bitten by a gnat of the genus *Culex*, the latter, no less than an Anopheles, sucks into its stomach all stages of the malarial parasite, but they are speedily digested, gametocytes and all. On the other hand the gametocytes of avian malaria are digested by Anopheles, but undergo further development in the stomach of Culex.

The Sporozoa that infest the blood corpuscles of various kinds of vertebrate animals are placed in a special order **Hæmosporidia**. In all those whose life history is accurately known, the trophozoite inhabits a red blood corpuscle, at least for a part of its existence, and becomes a schizont, which multiplies itself asexually by schizogony; the process is repeated for several generations till the host is thoroughly infected by the parasite. Then follows a sexual generation, consisting of gametes which conjugate and form zygotes. The zygotes are motile and seek out a suitable position in which to encyst. The encysted forms or oöcysts then divide into a large number of minute sporozoites, which are always naked and motile, never enclosed in sporocysts.

Different kinds of Hæmosporidia are found in all classes of Vertebrata, Fishes, Amphibia, Reptiles, Birds and Mammals; but, with one doubtful exception, they do not occur in Invertebrata. Those that attack cold-blooded Vertebrates do not appear to have any harmful effect upon their hosts, but those infesting Birds and Mammals produce all kinds of illness. Thus of the genus **Piroplasma**, *P. bigeminum* is the cause of the fatal "red-water" fever in cattle, and is trans-

mitted by the bites of ticks. *P. canis*, also transmitted by ticks, produces malignant jaundice in dogs, and *P. equi* is the cause of a fever similar to malaria in horses. These malignant and unfortunately too common little organisms have only been discovered and studied in recent years, and the life histories of many of them are still imperfectly known. They are so minute in size that the highest powers of the microscope and the most refined methods of histological technique are necessary for the elucidation of their structure. But it must not be supposed that because of their littleness they are not included in the domain of Natural History. In truth they form one of the most interesting chapters in the study of nature, and afford a striking example of those intimate relations between different animals which have been acquired, step by step, in the course of organic evolution, and by no means always to the benefit of all the animals concerned. It would be superfluous to insist on the practical importance of studies which enable us to cope successfully with some of the most virulent and dreaded diseases of man and domesticated animals.

"Διὸ δεῖ μὴ δυσχεραίνειν παιδικῶς τὴν περὶ τῶν ἀτιμοτέρων ζώων ἐπίσκεψιν. ἐν πᾶσι γαρ τοῖς φυσικοῖς ἔνεστί τι θαυμαστόν." *

* "Wherefore one should not be childishly contemptuous of the study of the most insignificant animals. For there is something marvellous in all natural objects."—ARISTOTLE, *De Partibus Animalium*, i. 5.

CHAPTER IX

THE FLAGELLATA—EUGLENA VIRIDIS, COPROMONAS SUBTILIS, AND POLYTOMA UVELLA

It was known to the earliest microscopists that water containing organic matter in solution soon becomes tenanted with swarms of microscopic animalcules, and that of these different kinds succeed one another in a more or less regular order. The first stage is that of putrescence, a phenomenon due to the development of a vast number of Bacteria, which after a time become quiescent, form spores, and seem to disappear. They are succeeded by swarms of other animalcules of larger size, usually characterised by the possession of one or more relatively long, transparent and very fine processes of protoplasm, which by their lashing movements propel the organisms through the water. These protoplasmic processes have been aptly likened to whip-lashes, and hence the organisms possessing them have been called the **Mastigophora**, or whip-bearers, whilst a subdivision of the group is known by the name of the **Flagellata**. One of the commonest as also one of the largest of these forms is an animalcule of a deep green colour, which is frequently found in such abundance in puddles of rain-water impregnated with decaying vegetable matter that the water appears of a uniform dark green tint, easily distinguished from the green colour imparted to ponds by the presence of filamentous algæ, since the latter are visible to the naked eye when a glass vessel containing them is held up to the light. Our animalcule, indistinguishable by the naked eye, is known as **Euglena**. There are many species of Euglena, differing in the shape and proportions of their bodies, but agreeing in all essential particulars with the species called **Euglena viridis**, which we will take as a type. An individual of this species has the form depicted in fig. 40. Its body consists of a single elongated cell, tapering to a point at one extremity. The opposite extremity is blunt and obliquely truncated, and, as it

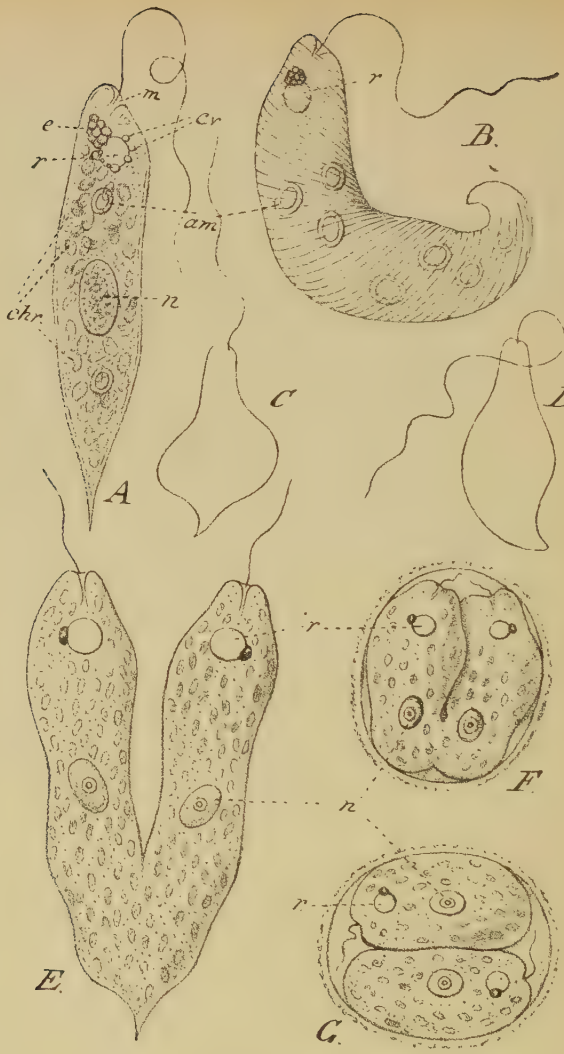

Fig. 40.

A, *Euglena viridis*; *m*, the so-called mouth; *n*, the nucleus; *e*, the stigma; *r*, reservoir; *c.v.*, contractile vacuoles; *chr*, chromatophors; *am*, pyrenoids with sheaths of paramylum. *B*, another specimen, showing change of shape and diagonal striation of the cuticle. *C* and *D*, outlines to show various stages of contraction. *E*, a free swimming specimen undergoing longitudinal division. *F* and *G*, division of an encysted form. (*A-D*, original; *E-G*, after Stein.)

is always directed forward in swimming, it may be called the anterior end. From it projects a single thread-like transparent process of protoplasm in which no definite structure can be made out even with the highest powers of the microscope. This process is the **flagellum**, and although it presents no obvious structure, it is highly contractile, and when the animal is in active movement executes a series of rapid bending movements, which can best be compared to the motion of the finger in beckoning. By these movements of the flagellum the organism is propelled through the water in the direction of the flagellum, and the latter organ has sometimes been called a **tractellum**, because it draws the organism after it. Closer observation shows that the flagellum does not spring from the surface of the anterior extremity, but emerges from a conical depression situated somewhat excentrically on the blunted snout-like end. The flagellum originates from one of the walls of this depression and clearly is a process of the ectoplasm, since it cannot be traced deeper than the most external firmer layer of the protoplasmic body. Though *Euglena viridis* has the characteristic shape here described, it is eminently contractile, and therefore capable of considerable change of shape. An individual, if watched for a short time, may be seen to go through the various phases of contraction shown in fig. 40. Now it is swelled up at the hinder, now at the anterior extremity, and now it is swelled up in the middle so as to resemble a top. These contractions are combined with sinuous worm-like movements, the whole being so characteristic that the name "euglenoid" is applied to them, a word often used in describing the similar movements of Monocystis. Just as in the last-named genus we saw that the contractile power resided in a specialised external layer, the ectoplasm, so we find that the cell-body of Euglena is composed of an external layer of firmer and denser ectoplasm, whilst the central more fluid portion of the cell-body is known as the endoplasm. In addition to the ectoplasm, Euglena is clothed by a delicate external cuticle, which is continued at the anterior end into the conical depression from which the flagellum springs. This cuticle exhibits a number of fine oblique parallel striations, which are thought by some authors to be the seat of the contractile movements—to be specially differentiated fibres of contractile protoplasm. This, however,

can hardly be the case, since the cuticle can easily be isolated by crushing the organism, and then the striae can be seen to be thickenings of the cuticle and not differentiations of the ectoplasm. The cuticle is obviously very elastic, or the euglenoid movements would be impossible.

The nucleus of Euglena is a spherical vesicular body, containing a darker spot called, but probably incorrectly, the nucleolus. The nucleus maintains a constant position about one-third of the whole length of the animal from its hinder end. Its structure will be described in detail when we come to consider the reproductive process.

One of the most striking characteristics of Euglena is its green colour. Viewed with a low power of the microscope, the cell-body appears uniformly green, with the exception of the blunt anterior extremity and the flagellum, which are colourless. But examination with a higher power shows that the green tint is due to the presence of a number of circular or oval discs, known as the **chromatophors**. In many species of Euglena the chromatophors lie in an even layer immediately under the external surface, and, since they do not change their position, it is probable that they are embedded in the ectoplasm. In *Euglena viridis*, however, the chromatophors radiate outwards from a heap of granules, situated in the centre of the body. The green colour of the chromatophors is due to the presence of chlorophyll, each chromatophor consisting of a matrix of protoplasm of firm consistency, through which the chlorophyll is evenly diffused. Just as green plants are able, through the agency of their chlorophyll corpuscles, to decompose the carbonic acid in the air, setting free oxygen and combining the carbon with water to form starch, so Euglena is able through the agency of its chromatophors to decompose carbonic acid, but the product is not starch but an allied body of the same chemical composition—viz. $C_6 H_{10} O_5$. This substance, called *paramylum*, differs from starch in several respects, particularly in giving no colour with iodine, whereas starch gives a deep blue colour.

When Euglenæ are kept in a vessel in bright sunlight, bubbles are abundantly formed in the water in which they are contained, and these bubbles, if collected, can be shown to consist of oxygen. At the same time the heap of granules from which the chromatophors radiate can be seen to have

increased in size. On the other hand, if Euglenæ are kept in the dark the granules diminish. These granules consist of paramylum, and they are arranged round a central corpuscle of rather dense proteid material, which is considered to be equivalent to the proteid structures found in many Flagellata, and known as **pyrenoids**. True pyrenoids are found in only a few of the green Euglenoids, and when present they are always closely associated with the chromatophors. For every chromatophor there is a single pyrenoid, projecting from its surface, and consisting of a central proteid mass surrounded by a sheath of paramylum. In some other Flagellates the sheath consists of true starch. It should be noted with respect to both chromatophors and pyrenoids, that these minute components of cell structure behave in certain respects like cells themselves. They never arise independently, but always as a result of the division of pre-existing bodies of the same nature; pyrenoid arising from pyrenoid, and chromatophor from chromatophor. Hence there are authors who would carry Virchow's aphorism still farther (see p. 111), and would say not only "omnis cellula e cellulâ," but also "omne granulum e granulo"; a generalisation true enough for the bodies we have just been considering, but not yet applicable to all the kinds of granules found in cells.

From what precedes it is obvious that in its nutrition Euglena differs from animals in general, and resembles the vast majority of plants. The question is whether its plant-like or, as it is called, **holophytic**, mode of nutrition is supplemented by the true animal mode of ingesting solid food, called **holozoic** nutrition? It has been asserted that the action of the flagellum causes a vortex in the small conical depression from which it springs, and that minute particles of solid matter, swept in by the vortex, are ingested by the Euglena and serve as food. Hence the opening has been styled a mouth, the depression a gullet. But, as a matter of fact, there is but one well-authenticated instance of the ingestion of solid food by a green Flagellate, and that not by a Euglenoid, but by a species known as *Chrysomonas flavicans*. On the other hand, it would seem that in Euglenæ the holophytic nutrition is supplemented by another mode known as **saprophytic**. It has been observed that Euglena will live and apparently flourish in complete darkness for as long as thirty-nine days, and, as chlorophyll is

only active in sunlight, this raises the presumption that the organism is able to obtain food in some other way. Experiments have shown that if they are kept in carefully filtered water Euglenæ will not flourish, even in the sunlight, but that they will recover on the addition of small quantities of albuminous matter to the water. Hence it is concluded that they absorb organic substances in solution by the whole surface of the body, and it is supposed that during the daylight they form paramylum, and during the night they absorb organic food in solution. It must be confessed, however, that there is no very satisfactory evidence on the subject of the nutrition of Euglena, except the well-established fact that it decomposes carbonic acid and forms paramylum.

A noticeable feature in Euglena is the presence of a speck of bright red colour immediately behind the anterior end of the body and close to the inner end of the conical depression called the gullet. This spot is the **stigma**. It has a somewhat quadrangular outline, lies close against a spherical clear cavity which will be described in connection with the contractile vacuoles, and consists of a meshwork of plasma, containing a number of minute red granules composed of a substance called **hæmatochrome**. This red pigment is common in many flagellates, and it is particularly abundant in a red species known as *Euglena sanguinea*. It becomes blue-black with iodine, is soluble in ether or alcohol, but is not affected by ammonia or acetic acid. According to a recent author the stigma is covered anteriorly by one or more strongly refracting granules of paramylum, and the whole structure serves as a rudimentary organ of vision, the paramylum granules forming the lenses, the stigma the percipient elements. It is at the best doubtful whether the stigma is specially sensitive to light, but it is significant that the hæmatochrome disappears in individuals kept in the dark, and that it has the same reactions as the pigments found in the eyes of many higher animals.

The clear vesicular space against which the stigma appears to be flattened has often been confused with the contractile vacuole. It is not, however, contractile, but serves as a chamber or reservoir into which several minute contractile vacuoles discharge their contents. These minute contractile vacuoles have much the same structure as in Amœba; there may be one only, or several, as in *Euglena viridis*, and when

there are several they contract in succession. The reservoir into which they discharge is in connection with the hinder end

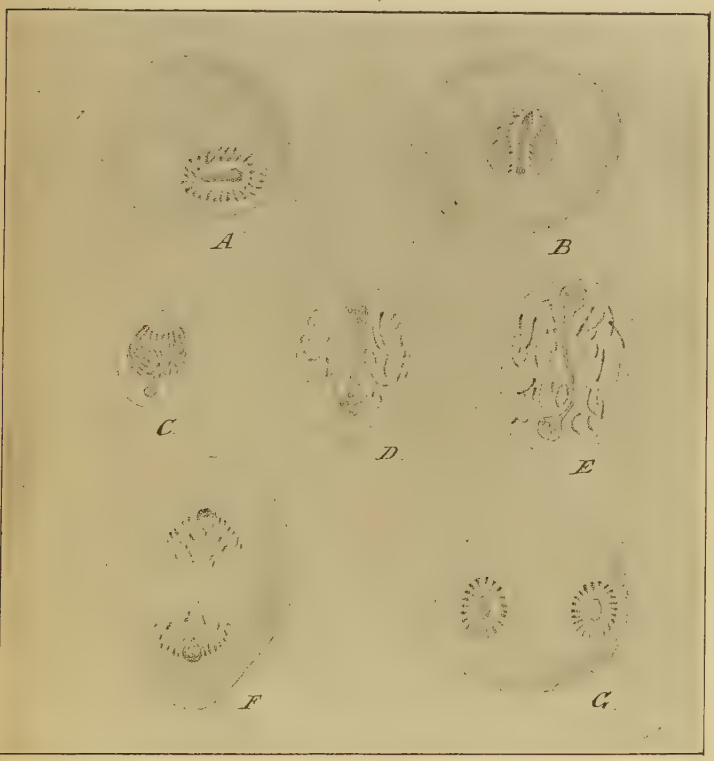

Fig. 41.

Mitosis in Euglena. *A*, elongation of the nucleocentrosome, radial arrangement of the chromosomes. *B*, further elongation of nucleocentrosome; pennate arrangement of chromosomes. *C*, chromosomes arranged in a ring round the dumbbell-shaped nucleocentrosome. *D* and *E*, the chromosomes split and their halves travel in opposite directions. *F*, final stage of mitosis. *G*, reconstitution of the daughter nuclei. (After Keuten.)

of the so-called gullet, and slowly empties its contents into it. *Euglena viridis*, if kept sufficiently long under observation,

may be seen to multiply by binary division, the plane of division always passing through the long axis of the body. Transverse division has never been observed in any species of Euglena. The division of the body begins at the anterior, and passes gradually to the posterior end, so that in the middle of the process one sees two organisms joined together, and it would be difficult to say, if one did not follow it to the end, whether there were two individuals conjugating or one individual dividing. Division of the cell-body is accompanied by division of the nucleus, which goes through a peculiar form of mitosis. It has already been said that the nucleus lies nearer the posterior end of the body, that it is of oval shape, and contains in its centre a body generally described as a nucleolus ; but, as its behaviour differs from that of an ordinary nucleolus, it will be best to call it by a special name—viz. the **nucleocentrosome.** The nucleocentrosome itself stains intensely with certain aniline dyes, but not with those which ordinarily stain chromatin, and thus it can easily be differentiated from the true chromosomes, which are rod-like structures arranged radially around it, and are so small and so numerous that they cannot be counted. A nuclear membrane is present. Preparatory to division the nucleocentrosome elongates and becomes dumbbell-shaped, and the chromosomes are at first disposed with regard to it like the barbs of a feather to its axis. Eventually, as the nucleocentrosome continues to elongate, the chromosomes come to lie parallel with it, and when it assumes the shape shown in fig. 41, *C*, they are collected in a ring round the middle of the fine thread which connects its now swollen ends. At this stage the chromosomes split longitudinally, and eventually their halves separate and travel to the opposite ends of the nucleocentrosome. The thread connecting the two ends of the latter then breaks, the whole nucleus divides, and the chromosomes take up a resting position around the two new nucleocentrosomes. The whole process of mitosis goes on inside the nuclear membrane, as is common in Protozoa, and the nucleocentrosome appears to take the place, or, at any rate, to fulfil the functions, of the centrosomes in normal mitosis. Previous to division, the flagellum of Euglena is doubled ; not, it would appear, as the result of the splitting of the original flagellum, but by growth of a new one.

It is not known whether there is any limit to the power of

multiplication by longitudinal binary division in Euglenæ, but probably there is, for at times the individuals come to rest, absorb or cast off their flagella, and each becomes rounded and surrounds itself with a gelatinous cyst wall of some thickness. Often great numbers of Euglenæ may be observed in this encysted condition, and, the cysts of adjacent individuals fusing together, they form a scum on the surface of the water, or at the bottom around stones and other objects. After a period of quiescence the encysted organism divides longitudinally, the nucleus passing through the mitotic changes already described. Usually there is only one division, and its products, after developing flagella, escape from the cyst and swim off as young Euglenæ. But it not infrequently happens that after the first division each of the daughter products secretes a new cyst for itself within the parent cyst, and rests awhile. Each may then divide, so that four cells are formed within the parent cyst, and these four may develop each one a cyst, and, after a further period of rest, divide again, forming eight. Usually the process does not go further, but the parent cyst and the daughter cysts burst, and the eight young Euglenæ are liberated. Occasionally, however, the parent cell has been observed to divide repeatedly without the formation of special daughter cysts, as many as thirty-two young Euglenæ being formed and eventually set free. A recent observer has described the formation of numerous flagellated young by the repeated division of an encysted individual, an observation which confirms the description given above of division into thirty-two.

Encystment, though commonly, is not necessarily followed by division. *Euglena viridis* not infrequently throws off its flagellum, surrounds itself with a gelatinous cyst wall, and, after a period of rest, develops a new flagellum and emerges to resume an active existence.

There is no well-authenticated case of conjugation in Euglenoids.

Our next example of the Flagellata, **Copromonas subtilis**, is one that has only very recently been discovered, but nevertheless is very common and easily procured. It lives in the fæces of frogs and toads, and large numbers can be obtained for study if the following instructions are carefully carried out.

A frog or toad is killed and its large intestine removed. The contents of the intestine should then be carefully pressed out into a small and perfectly clean glass dish, diluted with a small quantity of a freshly made solution consisting of 20 c.c. egg albumen, 1 gr. common salt and 200 cc. distilled water, and at once covered with a glass plate. The intestine should not be cut open, and care must be taken to exclude blood or intestinal epithelium from the culture, for if these are present bacterial putrefaction will be set up, which is inimical to the development of Copromonas. After some four or five days the diluted fæces will be found to be swarming with flagellate monads having the structure represented in fig. 42, *A*. The body of Copromonas is oval or pear-shaped, varying in length from 7·5 to 20 μ, and in breadth from 7 to 8 μ. The whole body is invested by a thin but rigid pellicle except at the narrower or anterior end, where there is a depression constituting a cell-mouth or **cytostome**, leading into a tube, the so-called **cytopharynx**, which extends backwards with a slightly spiral course and ends in the soft internal protoplasm somewhere about the middle of the body. Projecting from the cytostome is a single flagellum or tractellum, whose length is usually somewhat greater than that of the body. In well-stained preparations the basal end of the flagellum is seen to run for a short distance along the wall of the cytopharynx and to take its origin from a distinct basal granule. Under ordinary conditions Copromonas progresses forward with a slow even movement due to the beckoning action of the anterior part of the flagellum, but does not exhibit any euglenoid movements. The pellicle is rigid and non-contractile, and as long as the animal is in a healthy condition the contours of its body remain constant. When stimulated the whole of the flagellum is thrown into vibrations, and the animalcule is able to turn in its course by bending movements of this organ.

As in Euglena the base or root of the flagellum is in close relation to a relatively large vacuolar space, which is not a contractile vacuole but a **reservoir**. The contractile vacuole is single or rarely double, minute, rhythmically contractile, and situated at the side of the reservoir farthest from the flagellum. It discharges its contents, at intervals of about half-a-minute, into the reservoir, and the latter would appear to slowly void its contents into the cytostome.

Whereas it is at the best doubtful whether Euglena ever ingests solid particles as food, there is no doubt that the nutrition of Copromonas is holozoic and that the cytostome is a true cell-mouth. All sorts of bacilli, micrococci and other organic particles are drawn into it, and pass down the cytopharynx, but only the smaller particles are taken into the protoplasm at the hinder end of the latter structure; the larger bacilli and bacteria are rejected and returned to the exterior through the cytostome. The minute particles that are ingested at first lie in the protoplasm at the bottom of the cytopharynx without any vacuole surrounding them, but presently they become agglutinated into balls and surrounded by food vacuoles. In this condition they are aggregated in the hinder part of the body and slowly digested. The progressive stages of digestion are indicated by the different colour reactions given by such an *intra vitam* staining reagent as neutral red.

The nucleus lies in the posterior half of the body, and is not connected in any way with the flagellum as is often the case in Flagellata. In stained specimens it is seen to consist of a central deeply staining mass surrounded by a clear non-stainable zone, which in turn is bounded by the nuclear membrane. The central mass seems to consist of an achromatic substance containing variously sized granules of chromatin, and achromatic threads radiate across the clear zone, connecting the central body with the nuclear membrane.

The monads whose structure and habits have just been considered may be observed to multiply rapidly by longitudinal division for some four or five days of their existence in the medium in which they are cultivated. Towards the end of this time—but no definite time limit can be assigned, for the period is apparently very variable—a number of them are found to be conjugating in pairs, and for the next three or four days conjugating couples are more numerous than individuals undergoing division. Many of the zygotes resulting from conjugation become encysted and pass into a resting condition, but others continue to lead an active life and reproduce themselves asexually by division. Hence it is clear that the whole life cycle of Copromonas is divisible into two periods, the one asexual and the other sexual. In fig. 42 the asexual period is represented by the upper circle, the sexual period by the lower circle.

Fig. 42.

A series of figures arranged to illustrate the life cycle of Copromonas subtilis. The upper circle indicates the course of the asexual period, the lower circle the sexual period of the life cycle. The central figure *A* illustrates the structure of the free swimming individual *B*, an early stage of division : two new flagella are sprouting from the anterior end and the nucleus is drawn out into a dumbbell shape. *C*, a later stage of division : the reservoir is divided and the two ends of the nucleus are connected by a fine thread. *D*, division nearly completed. Starting again from *A* and going round the lower circle : *2*, two individuals or gametes are fusing together by their anterior ends ; one flagellum is being drawn in. *3*, further fusion of the gametes ; on the left a nucleus in an early stage of division ; on the right the first reduction division of the nucleus nearly complete. *4*, further nuclear reduction by a heteropolar division ; parts of the first reduction nuclei are seen degenerating below. *5*, fusion nearly complete ; two reduced nuclei are present. *6*, a zygote before encystment ; the nuclei are not yet fused. *7*, a resting cyst with a single conjugation nucleus. *8*, a young monad shortly after liberation from a cyst. *1*, a zygote derived from stage *5*, the nuclei are fusing and the organism is assuming the motile form ; it will develop into *A*, and after passing through some generations of asexual production its progeny will encyst and return to stage 7. (After C. C. Dobell.)

During the asexual period the monads feed greedily and grow to a large size before division. An individual about to enter on division becomes sluggish in its movements, and its flagellum, waving about languidly the while, is gradually withdrawn into the body until it disappears altogether. While the flagellum is being withdrawn the cytostome and cytopharynx also become indistinct, and appear to close up and become obliterated. Meanwhile the nucleus has been undergoing changes. It elongates in a direction transverse to the long axis of the body, and first becomes fusiform and subsequently dumbbell-shaped (fig. 42, *B*), the latter shape being due to the massing of the chromatin particles at the two ends of an elongated achromatic band. In a short time two new flagella make their appearance at the anterior end. At first they are minute peglike outgrowths, but they soon increase in length and as they do they begin to execute the characteristic lashing movements, as a result of which the erstwhile indolent dividing monad again becomes active. A cleft now makes its appearance at the anterior end between the bases of the sprouting flagella: first it cuts the reservoir in two and thence extends gradually backwards till it divides the animalcule longitudinally into halves. While these changes are in progress the dumbbell-shaped nucleus of the earlier stage assumes the shape shown in fig. 42, *C*, and finally the thread connecting the two chromatin masses breaks and the latter become rounded off to form the nuclei of the two daughter-monads. The nuclear division is therefore amitotic. The cytostome and cytopharynx appear to be formed anew in each product of division. It is evident that a moiety of the reservoir of the parent form goes to each daughter form, but the contractile vacuole of the parent persists and passes over to one of the daughter forms, the other developing a new contractile vacuole.

It is not clear what is the limit, or what imposes a limit, on the capacity of a swarm of Copromonas to reproduce asexually by binary division. It may be due to an exhaustion of the food supply, or to a chemical change in the medium in which they are living, or to an inherent incapacity to reproduce themselves asexually for more than a certain number of generations; but whatever the cause, after a period varying from two to six days, the monads begin to conjugate. In

this act any two individuals of a swarm may unite together. Every free schizogonous individual of Copromonas is therefore a potential **gamete**, and since the members of any conjugant couple are indistinguishable in shape and structure, and as variable in point of size as are the individuals composing the swarm, there is no recognisable distinction of sex, and the gametes are **isogametes**.

The sequence of events is as follows. Two gametes approach one another, come into contact by their anterior ends, and soon become firmly united together. The flagella of both continue to move actively, but one soon becomes shorter, and at the end of a quarter of an hour or more is completely withdrawn. Fusion of the bodies of the two gametes gradually extends backwards, as shown in fig. 42, *3* and *4*, until the resulting **zygote** has the appearance of a single asymmetrical individual (fig. 42, *5*). After a time the body of the zygote is remodelled so that, although noticeably larger, its contours are exactly those of the ordinary free swimming form. The nuclear changes accompanying these processes are of some importance as an illustration of the rule that reduction of the chromatic contents of the nucleus takes place prior to the union of the nuclei in conjugation. No change is observed in the nuclei of the gamete until a considerable degree of cytoplasmic fusion has been effected. The nucleus of each then divides amitotically into two sub-equal portions (fig. 42, *3*), and in each case one of the products of division, distinguishable from the first because of its paler colour in stained preparations, rapidly degenerates and soon breaks up and is absorbed into the cytoplasm. At a later stage (fig. 42, *4*) a second reduction of the chromatin of each nucleus is effected by the extrusion of a small granule which similarly degenerates in the cytoplasm. Though not certain, it is highly probable that only one such granule is ejected from each nucleus, and the process may be described as an asymmetrical or **heteropolar** division of the nucleus, one of the division products being much smaller than the other. When the bodies of the two gametes are nearly completely fused, the two nuclei approach one another and for some little time lie side by side with their nuclear membranes in contact, but eventually the adjacent membranes are absorbed and the two chromatin masses are completely fused together. It seems that, just as was the

case with the flagella, the reservoir, cytostome and other organellæ of one gamete are absorbed, but of the other persist during and after conjugation.

In most flagellates conjugation is followed by encystment, but Copromonas is exceptional in this respect, that some of the zygotes retain their flagella and other organellæ, continue to lead an active existence, and after the lapse of a certain time begin to reproduce themselves asexually by longitudinal division. It would appear, however, that sooner or later the progeny of these scissiparous zygotes pass into the encysted condition. The more normal course is for the zygote to encyst itself shortly after conjugation. In this case it becomes more rounded in shape, and decreases in size. The flagellum is gradually drawn in, the movements of the animalcule cease and a cyst-wall is formed round its body. At first the cyst-wall is very delicate and not easily seen, but afterwards it becomes thicker and of a gelatinous consistency, and eventually forms a hard resistant coat.

As living Copromonads are not found in the rectum of the frog, but may invariably be obtained from a suitable culture of the fæces, the life history of the species is evidently as follows. The resting cysts are scattered in damp places, are washed down into pools and streams, and are casually swallowed by a frog or toad along with its food. During their passage through the alimentary tract the resistant cyst-walls are dissolved, and on arriving in the rectum the monads are ready to escape. When the fæces are passed to the exterior and diluted with water (for they are sure to be deposited in damp places) the monads emerge and for a time live in the diluted medium suitable to their active existence and multiply rapidly by division. But from the nature of the case the conditions favourable to their active existence cannot last long. The monads therefore conjugate, and the resulting zygotes encyst. The cysts are scattered, are again swallowed by a frog or toad and thus the cycle is completed. But if a zygote should be placed in conditions favourable to active existence it has the power of continuing to feed and multiply by division until finally its progeny encyst and pass on to the normal cycle of the life history.

Polytoma uvella is a flagellate often found in long-standing

infusions of organic matter. In size it is somewhat smaller than Copromonas and in shape almost perfectly oval, with a pair of flagella of medium length projecting from one of its ends. Both flagella are used equally in swimming, and the animalcule darts with great rapidity through the water, pursuing a more or less definite course. The protoplasm of the body is invested by a delicate but distinct membrane or envelope, which it usually fills and fits against so closely that the latter is difficult to see. But if the organism is badly

Fig. 43.

Polytoma uvella. *A*, an individual showing the envelope and contained protoplasmic body, central nucleus, stigma, two flagella, two contractile vacuoles, and posterior starch granules. *B-F*, successive binary divisions within the envelope giving rise to four young Polytomæ.

nourished the protoplasm shrinks and the envelope becomes obvious. This fact shows that the envelope is not a simple differentiation of the most external layer of the protoplasm, but a true protective covering secreted by, but distinct from, the protoplasm. The two flagella project through pores in the envelope. The chemical constitution of the envelope is

not known, but it does not give the reactions of cellulose. There is no mouth, but two contractile vacuoles may be seen close to the bases of the flagella. A nucleus is placed near the hind end of the body, and generally a small stigma or nodule of hæmatochrome may be distinguished in the anterior half of the body. Though Polytoma has no chromatophors, is colourless and devoid of chlorophyll, it has the power, usually possessed only by organisms which contain chlorophyll, of storing up amylum in its body. Close observation shows that the posterior half of every well-nourished individual is filled with small granules, which, when treated with iodine, give the characteristic reactions of starch. If a Polytoma is starved by being transferred to a liquid devoid of nutrient organic matter, the starch granules gradually diminish in size, and finally they disappear and the animal dies. The exact mode of formation of these starch granules is not understood. They are not ingested, for Polytoma has no mouth, and has never been seen to ingest solid particles, nor are any foreign matters excepting these starch granules to be seen in its protoplasm. Its nutrition must be described as saprophytic, for it lives immersed in a nutrient fluid, and imbibes it by the whole surface of its body. It evidently does not get its carbon from carbon dioxide, for, as we have just seen, it becomes enfeebled and dies if it is taken from the nutrient solutions in which it lives, and therefore it must form starch in some other manner than its chlorophyll-containing relatives. Now, in the higher animals a form of amylum, known as *glycogen* or animal starch, is found in some abundance in the liver and in muscle. Numerous experiments have shown that glycogen is formed, in the dog for instance, when the animal is kept on an exclusively proteid diet, and it is therefore proved that starch may be formed by the activity of living tissue from proteid material. It cannot be doubted that the protoplasm of Polytoma has this same power of converting the albuminous substances which it absorbs from organic solutions into starch. Attention should be paid to the existence of starch in *Polytoma uvella*, for it is sometimes incorrectly said that organisms devoid of chlorophyll never contain starch. Polytoma reproduces itself by a process of continued division within the cell envelope, either in the free swimming or in a resting condition. The act of division may nearly always be seen in individuals which are kept

under continuous observation. In a free swimming form the nucleus divides mitotically, and a transverse constriction of the protoplasmic body follows, not involving the envelope. The two flagella of the parent form remain attached to the anterior product of division and the organism continues to swim about actively, consisting now of two cells lying inside a common membranous envelope, the more anterior of the two cells alone bearing flagella. The next division is at right angles to the first, and therefore parallel to the long axis of the original parent cell. Four cells are thus produced, still enclosed within the envelope of the original parent form, and still the two flagella are active and attached to one only of the four daughter-cells. Another division may take place, producing eight daughter-cells, but more usually when four cells are formed the maternal flagella are withdrawn, each of the four cells acquires a new pair of flagella, the envelope in which they are contained is dissolved, and they are set free as four young Polytomæ, each of which acquires a new envelope on liberation. This process is repeated again and again for a period of from four to six days, by which time the reproductive activities seem to be exhausted and to require a stimulus for their renewal. This stimulus is afforded by the act of conjugation. The Polytomæ come together in pairs, each individual of a pair constituting a **gamete**. The gametes fuse, nucleus with nucleus and cell-body with cell-body, and form a spherical **zygote**, which surrounds itself with a thick envelope and passes into a resting condition. After a time the zygote divides into two, each of the two again divides, and the four cells thus produced divide once again, so that eight cells are formed within the cyst wall. Each of the eight cells develops a pair of flagella, the thick cyst-wall is dissolved, and the eight young Polytomæ emerge to resume an active existence. They divide, usually into four, in the free swimming condition, and the life cycle is repeated. Occasionally a free swimming Polytoma will throw off its flagella, secrete a thick envelope, and pass into a resting stage without conjugation. In this case no division of the contents of the cyst has been observed.

In both Polytoma and Copromonas, the reproductive power seems to become exhausted after a period of repeated multiplication by division. We shall see in the next chapter that

this is a very common phenomenon amongst the Protozoa, yet it cannot be called a universal one, since we have been unable to record any exhaustion following upon repeated binary fission, either in Amœba or in Euglena. In neither of these forms does it appear to be necessary that at regularly recurring periods individuals should conjugate to form zygotes which, after a period of rest, enter upon a new lease of reproductive life. Yet the phenomenon of conjugation is so common both in the lower plants and animals that we are tempted to believe that it is a very necessary condition of existence and that it has simply been missed, that we have failed to observe it, in the forms in which it is not recorded. We have seen that it plays a very important part in the life cycles of Monocystis and Plasmodium, that the nuclei of the cysts of Actinosphærium conjugate in a very peculiar way in couples, and that there is a somewhat similar fusion of the nuclei in couples in the Mycetozoa. In some of these forms the conjugating individuals or **gametes** are perfectly similar, but in others they exhibit a more or less marked dissimilarity and forecast in a greater or less degree the differentiation of sex which is so characteristic both of the higher animals and plants.

Polytoma uvella is colourless and devoid of chlorophyll, but the majority of its nearest allies are green, having one or more chromatophors containing chlorophyll. Their nutrition is holophytic, and they are so plant-like in structure and in function that they are always described as plants in botanical works. Yet the zoologist, recognising their affinities to Flagellata, whose behaviour is clearly animal, cannot afford to leave them out of consideration, and hence they are classed in zoological works under the name **Phytomastigoda**, or plant-like Flagellates. Some of them are of so much interest and importance that they must engage our attention for a while.

CHAPTER X

THE VOLVOCINÆ

The three genera, **Pandorina**, **Eudorina**, and **Volvox**, are of special interest because they form a progressive series of increasing complexity both in their organisation and in their mode of reproduction. All three are found in stagnant water. Whereas in the Protozoa which we have hitherto studied the products of cell division separate sooner or later from one another and lead a free and independent existence as separate cells, or, as is the case in Badhamia, the cells after a short period of separate existence fuse together and form a plasmodium in which the cell outlines are no longer distinguishable, we find in the Volvocinæ that a certain number of the cells remain adherent, and form a cell-colony.

One of the simpler forms of these colonies is illustrated by **Pandorina morum**. The unit of organisation is an ovoid cell, much resembling Polytoma in form, since it is furnished with a pair of flagella of equal length, a membranous envelope, a contractile vacuole, a stigma composed of hæmatochrome, and a vesicular nucleus. It differs, however, from Polytoma in possessing a large chromatophor coloured green with chlorophyll. These units, instead of living separately, are aggregated together to form a simple colony composed of sixteen, more rarely of thirty-two, similar individual cells. The colony is spherical or oval (fig. 44, *A*); the cells composing it are wedge-shaped, their broader ends external, their pointed ends meeting together in the centre of the colony. Each cell has its own membranous envelope, but in addition there is a colonial envelope of like structure and composition in which the individual components are embedded. The colony swims about by the united action of the flagella of its members, and its nutrition is holophytic.

Multiplication of the colony is effected in two ways. The

first and simpler method is by continued binary division of all the units composing the colony. Each cell divides into

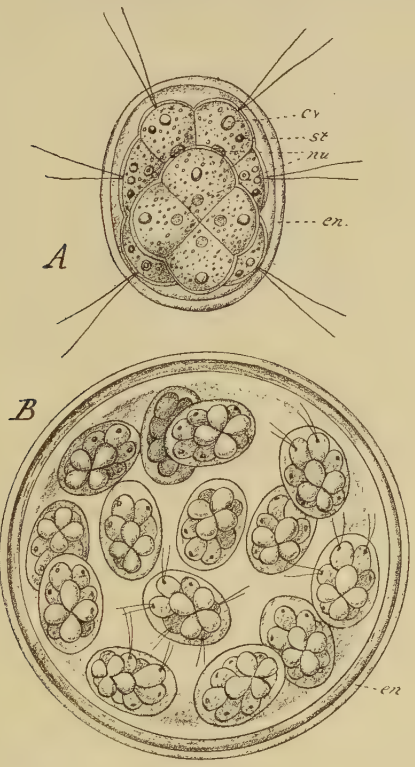

Fig. 44.

Pandorina morum. *A*, a colony of sixteen flagellated cells enclosed in a common colonial envelope. *B*, a colony in which the cells have given rise by repeated binary division to daughter colonies, still enclosed in the common colonial envelope; *cv*, contractile vacuole; *st*, stigma; *nu*, nucleus; *en*, colonial envelope. (After Stein.)

two, the two into four, the four into eight, and the eight into sixteen. The colonial envelope is gelatinised and finally

dissolved, as also are the envelopes of the individual mother cells of the daughter colonies. Thus each daughter group of sixteen is set free, develops new cell envelopes and a new colonial envelope, and forms a free swimming colony.

After repeated multiplication by this means a generation of Pandorina colonies arises which enters upon a process of conjugation before reproduction. Preparatory to this process the sixteen individuals of a colony divide each into eight cells, the mother colony ceases to swim, falls to the bottom, loses its flagella, and the colonial as well as the individual membranous envelopes gelatinise and are dissolved. The dissolution of the envelopes proceeds slowly, so that it is some time before the groups of eight cells, formed by division of the sixteen cells composing the original colony, are set free. But eventually each member of a group develops flagella and an envelope and escapes as a single free swimming gamete. Two gametes meet by their anterior ends and conjugate, fusing completely with one another to form a zygote, which at first bears the four flagella of the two united gametes. Presently the flagella are cast off, the zygote surrounds itself with a thick envelope of red colour and enters into a resting stage. Before it develops further it it necessary that the zygote should be dried, which normally takes place when the pool of rain-water in which it lives becomes dried up in the summer. When the pool fills again after rain the zygote develops. Its envelope thins out on one side and forms a projection from the surface which breaks through and allows the zygote to escape in the form of a naked cell, which immediately develops flagella and an envelope, divides into sixteen adherent cells surrounded by a colonial envelope, and thus a new Pandorina colony is produced.

It is not certain whether there is any differentiation between the gametes of Pandorina. It appears that there are larger and smaller colonies, producing larger and smaller gametes, and also forms intermediate in size between these. It is stated that the larger gametes never conjugate with one another, but that the smaller and middle-sized gametes conjugate with the larger and also with one another. If this is the case, there is at the most the beginning of a differentiation into macrogametes and microgametes, or, as we may say, into female and male forms, in Pandorina.

Eudorina elegans is not very different in structure from

Pandorina. Its colonies, measuring from ·1 to ·15 mm. in diameter, are spherical or oval, composed of thirty-two, rarely of sixteen cells, which differ from those of Pandorina in being rounded, embedded at some distance from one another at regular intervals in the colonial envelope, and in the fact that their inner ends do not reach to the centre of the colony (fig. 45). The colonies multiply by repeated division of their

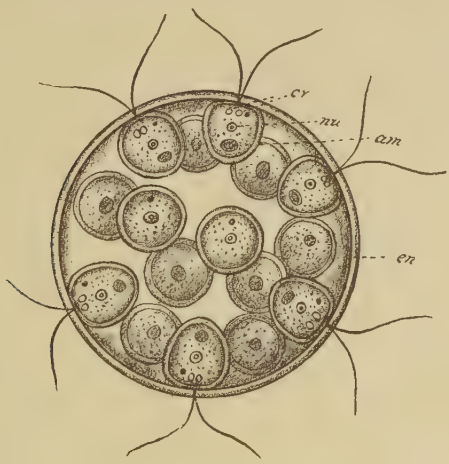

Fig. 45.

Eudorina elegans. The colony consists of thirty-two flagellate cells, situated at some distance from one another, and enclosed in a common colonial envelope. *cv*, contractile vacuoles; *nu*, nucleus; *am*, amylum bodies; *en*, colonial envelope. (After Stein.)

component individual cells, so that daughter colonies are formed much in the same way as in Pandorina. The process of cell-division is somewhat different, but the details need not be considered here. During the formation of the daughter colonies the envelope of the mother colony becomes very thin, and eventually it bursts and liberates the daughter colonies already provided with their flagella and colonial envelopes. After multiplying for several generations in this manner a generation of Eudorina colonies appears, the members of which do not differ in structure from ordinary colonies, but show a

marked differentiation in the course of their further history. Certain of these colonies, which we may speak of as female colonies, consist of thirty-two cells which we may call **macrogametes**, differing from the normal only in their somewhat larger size, and oval in shape. The remaining colonies undergo a process of cell-division leading to the formation of male cells or **microgametes**. Each individual cell of a male colony divides to form a flat plate composed of sixteen or thirty-two yellow cells which become rounded, and secrete an external gelatinous wall round the plate. Gradually these cells become elongated and spindle-shaped, they develop each a pair of flagella at one end, and may now be called **microgametes**. All the flagella of the cells composing a plate are turned in the same direction, and eventually the composite plate moves about by the action of its flagella, bursts out of the parent envelope, and swims freely in the water. Meanwhile the female colonies have come to rest (though their flagella remain attached and execute slow waving movements), and their colonial envelopes swell up and become gelatinised. When a free swimming plate of microgametes meets a female colony in this condition it attaches itself to it, the plate is resolved into its component microgametes, and these bore their way into the gelatinised cyst-wall of the female colony. Each microgamete works its way towards a macrogamete and conjugates with it, the two fusing to form a zygote which immediately becomes enclosed in a thick cyst-wall. The further development of the zygote has not been followed, but it probably does not differ much from that of the zygotes of Pandorina.

In both Pandorina and Eudorina all the cells composing the colonies take their share in the reproductive processes, but in the latter there is a differentiation into male and female colonies, into microgametes and macrogametes, which, at the most, is only obscurely indicated in the former species. But in **Volvox** we find that a considerable advance has been made, for the cells composing a colony are differentiated into those which are nutritive but not reproductive, and those which are reproductive but not nutritive, or, as it is said, into **somatic** and **generative** cells. **Volvox globator** is tolerably common in ponds and ditches. It has the form of a hollow sphere of considerable size as compared to Pandorina and

Eudorina, measuring from ·2 to ·7 mm. in diameter. The wall of the sphere consists of a thick membranous envelope in which numerous cells, each provided with its own cell-envelope, are embedded. There may be as many as 12,000

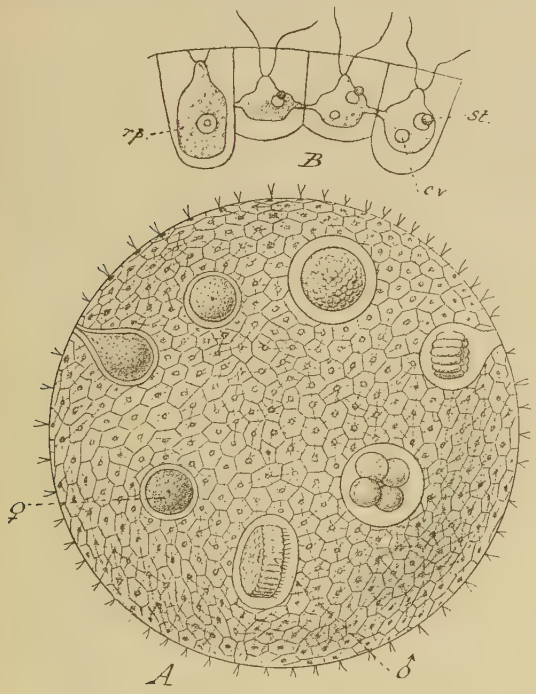

Fig. 46.

Volvox globator. *A*, a sexually ripe colony, showing microgametes ♂, and macrogametes, ♀, in various stages of development. *B*, a portion of the edge of the colony highly magnified, showing three flagellate cells united by protoplasmic threads, and a single reproductive cell, *rp.* *st*, stigma ; *cv*, contractile vacuole. (After Kölliker.)

of these cells. They form a single layer, and when viewed from the surface present the structure shown in fig. 46, *A*. The cell-bodies do not fill their envelopes, but are separated from them by a relatively considerable space, and every cell

envelope, pressed up against the envelopes of six adjacent cells, has a hexagonal outline. The bodies of adjacent cells are in direct organic continuity by means of fine processes of protoplasm, six of which radiate from every cell, perforate the centres of the six side-walls of the envelope, and are continued into the similar processes radiating from the six adjacent cells. Every one of these cells has a nucleus, a contractile vacuole, a chromatophor, an amylum body, and a pair of flagella, which last project from the surface of the colony and serve, in conjunction with the similar flagella of the other cells, as the locomotor organs of the colony. These ordinary or somatic cells multiply by division and thereby increase the number of units composing the colony, but they are unable to reproduce the colony. This function is limited to a small number of cells, distinguished from the somatic cells by their larger size and the absence of flagella. In *Volvox globator* eight of such cells are capable, by repeated binary division, of giving rise to new colonies, and, since this mode of reproduction is not preceded by conjugation, the cells in question are known as **parthenogonidia**. Without entering into the details of division, it may be stated shortly that the cell-body of each parthenogonidium undergoes repeated division within its special envelope, giving rise to a spherical colony which at first projects into the central cavity of the mother colony. Eventually the envelope of the parthenogonidium gives way, and the young Volvox, which has by this time developed flagella, falls into the cavity of the mother colony. Here it remains for a while, but finally escapes by rupture of the maternal wall. This method of asexual reproduction is continued for several generations, after which individual colonies make their appearance, differing from the normal asexual colonies in that they possess some fifty large non-flagellate cells which in their structure and size resemble parthenogonidia. Their fate, however, is different. Some of them simply increase in size, acquire a deep green colour, and project into the central cavity of the colony. These are the macrogametes or ova, and they are incapable of further development unless they are fertilised.

The microgametes or spermatozoa are formed from large non-flagellate cells which at first are exactly similar to those which give rise to the female cells. These cells divide

repeatedly, in much the same manner as in Eudorina, to form a flat plate or bundle of as many as 128 flagellate spindle-shaped microgametes. In *Volvox globator* the bundle now breaks up (the case is somewhat different in the closely related *Volvox minor*) and the microgametes pass into the central cavity of the colony. They swim by means of their flagella towards a macrogamete, and bore their way into its thick envelope. A single microgamete having passed through the envelope, fuses with the macrogamete, and the result is a fertilised ovum or zygote. The zygote surrounds itself with a double cyst-wall, not composed of cellulose, the outer wall being red and provided with spines and projections. The zygote itself forms a large number of starch granules in its protoplasm. A long period of winter rest follows, and in the spring the zygote develops by a repeated process of cell-division into a new Volvox colony.

The Flagellata are perhaps the most instructive group of the Protozoa. On the one hand they are connected with the lowliest forms of life, on the other hand they indicate, through the Volvocinæ, the transition from the uni-cellular to the multi-cellular condition, from Protozoa to Metazoa. It is specially important to note that certain members of the group, *Bodo angustatus* is an example, are able to assume an amœboid stage and to return again to the flagellate condition. Others, of which the genera **Mastigamœba** and **Mastigina** are examples, bear a typical flagellum but also put forth pseudopodia like a Rhizopod. When we consider further that the young of Badhamia and also the young of many Heliozoa (though not of Actinosphærium) are flagellate, we recognise that there is no sharp dividing line between the Rhizopoda and the Flagellata; the one form is capable of passing into the other, and there can be little doubt that they stand in the closest relationship to one another. Again, we see in the Flagellata organisms which are exclusively holophytic and indistinguishable from plants, organisms which are holozoic, and therefore unquestionably animals, and organisms which are saprophytic, and therefore resemble Fungi. We stand, as it were, in neutral territory, belonging to neither the animal nor to the vegetable kingdom, but inhabited by the natives of both. It is tempting to suppose that the Flagellata represent the group from which both animals and plants have sprung, but this we can hardly do. Were

such a supposition true we should expect the group to be still giving rise to new forms of animals and plants; for if it was capable of evolving higher forms in the past, why not in the present and the future? We have no evidence that the Flagellata are giving, or have recently given birth to new forms of higher organisation, and we must regard the living representatives of the group as possibly representing the early forms of life from which animals and plants sprung, but themselves so far specialised and adapted to particular conditions of life as to be now incapable of evolution outside the limits of their own special organisation. The Volvocinæ certainly suggest to us the successive steps through which the multi-cellular condition was evolved from the uni-cellular, and the importance of such a series cannot be over-estimated. But again, if we would be scientific we must be cautious, and we must not say that these are the steps through which Protozoa developed into Metazoa or Protophyta into multicellular plants. There is, in fact, no evidence that Volvox leads us any farther in the scale of organisation, and, indeed, there is some reason to suppose that in the Volvocinæ we have a line of evolution which has reached its acme in Volvox itself. The Flagellata suggests much, but they prove little, except that there are no distinct boundaries in living nature. A group which merges on the one hand into the Rhizopoda, on the other hand passes by insensible gradations into the multicellular condition; a group which belongs neither to the animal nor to the vegetable kingdom, but equally to both, brings to our minds the conviction of the unity of nature. And this idea, of the unity of organic life, is one of the most important in enabling us to apprehend the full meaning of the doctrine of Evolution.

CHAPTER XI

THE CILIATA—PARAMECIUM AND VORTICELLA

Though the Protozoa which we have studied present many differences of form and habit, none of them show any great complexity of structure. The Volvocinæ, indeed, seem to form an exception to this statement, but even in them the unit of organisation, the flagellate cell, is simple enough. We have now to consider a group of which the individual members, whilst retaining the characters of a single cell, attain to a very considerable degree of complication, and may be spoken of as being highly differentiated. But this elaboration of structure, be it clearly understood, is the outcome of specialisation of the protoplasm composing the cell-unit, and as such is different from that other mode of elaboration which, as we have seen in the case of the frog, is the outcome of the aggregation of many cells differing in kind and interwoven so as to produce tissues and organs of great complexity. In other words, the cell-body of the ciliate Infusorian is a microcosm; parts of it are differentiated for the performance of the several vital functions, whereas, in the higher multi-cellular animals, each component cell of a tissue is specialised for the performance of only one of those functions. Thus we may say that in the Ciliata the cell attains its greatest complexity of visible structure.

The species known as **Paramecium caudatum** and **Paramecium aurelia** are most conveniently selected for the study of ciliate structure and reproduction. Both are equally common and may nearly always be found in stagnant pools containing dead leaves and other decaying organic matter. Usually they are not very abundant in pools, but large quantities of them may easily be reared by collecting confervæ and water-weeds in summer weather, placing them in a jar of rain-water covered over by a glass plate and leaving them to rot. After a few days swarms of Paramecia will make their appearance and

may be transferred, by means of a pipette, to a nutrient medium. A suitable medium can be made by boiling hay in water, decanting off the liquid, and allowing it to stand. The infusion will soon be rendered turbid by the presence of Bacteria, and as Paramecia live on Bacteria, they will feed greedily and multiply with great rapidity.

Paramecium caudatum and *P. aurelia* are species so similar to one another that they have often been called by the same name. They are relatively large, attaining a length of ·3 mm., so that they are visible to the naked eye as whitish specks in the water when the glass containing them is held up to the light. We will confine our attention chiefly to *P. caudatum*, but the account given here will apply, as far as structure is concerned, almost equally well to *P. aurelia*. The latter species differs from the former principally in having two micronuclei instead of one,* and also its posterior extremity is rounded and blunt, whilst that of *P. caudatum* is pointed. A third species *Paramecium bursaria* is almost as common as the other two, but it is much less convenient for study, as its protoplasm is rendered opaque by the presence of numerous round green corpuscles, which are minute algæ living in the body of the infusorian and sharing its nourishment. The algæ, whilst they find protection in its body, are also of direct benefit to their host, for they manufacture starch through the agency of their chlorophyll, and from time to time their starch-laden bodies are swept into the endoplasm of the infusorian, are borne round in the food current, and digested. This intimate union of an animal and plant is paralleled in several other groups of the animal kingdom, and the phenomenon is technically called **Symbiosis.**

The first thing to observe in *Paramecium caudatum* is its shape: it preserves a perfectly definite and constant form as long as it is alive, never entering into an amœboid condition, nor exhibiting euglenoid or pseudopodial movements. It is, however, flexible and elastic, and may be observed to bend its body in passing round an obstacle, and to squeeze itself through an aperture smaller than its own diameter.

* It has, however, recently been stated that the possession of one or two micronuclei does not constitute a sufficient specific distinction between *P. caudatum* and *P. aurelia*.

The general shape of the animal is that of a spindle pointed at one extremity and rounded off at the other (fig. 47, *A*). It always moves with the blunt end foremost, so this may at once be distinguished as the anterior, the opposite pointed end as the posterior extremity. Further, it has a definite ventral surface indicated by a groove which begins as a shallow furrow at the anterior extremity and on the left, and curves over with a slight spiral twist towards the right, becoming narrower and deeper as it passes backwards. After traversing rather more than the anterior half of the body, the groove ends in the middle line in a relatively large and deep funnel-shaped depression leading into the soft protoplasm of which the centre of the body is composed. This depression is the mouth, or, as some authors prefer to call it, the **cytostome**, and the groove leading into it, the **peristome**. The anterior half of the body is slightly twisted in connection with the peristomial groove, somewhat as a leaden rifle-bullet is twisted after it is fired through a grooved rifle-barrel; and in consequence of this twist the animal spins round and round on its long axis as it swims through the water, a movement which makes it hard for a beginner to realise its exact shape.* If it is killed Paramecium swells out and loses its characteristic outlines. A living specimen, if its movements are not artificially restricted, moves about with great rapidity across the field of the microscope. It progresses in a tolerably straight course with a uniform velocity, very different to the jerky motions of a Flagellate. After going for some distance in one direction it stops, turns, seems to hesitate for a moment, and then darts off in a new direction.

These movements are entirely due to ciliary action. In a specimen which is held fast by pressure, or, better, by being placed in a thick solution of gum, the cilia can readily be seen all round the margins of the animal. They are all of equal size, except, perhaps, those at the posterior extremity,

* Paramecium may easily be kept still by the use of a freshly-made solution of gum-arabic. A few specimens should be placed in the smallest possible drop of water on a glass slide. A droplet of methylene blue or neutral red may be added to the water, and then a drop of fairly thick gum. The coverslip is now put on, and the animals are kept nearly still by the viscous mixture, but are not injured, and will live for some time and gradually be stained by the dye.

which are slightly longer than elsewhere, and completely clothe the external surface of the body. They extend also into the mouth and line the narrow tube through which the mouth opens into the endoplasm. Examination with a very high power of the microscope shows that the cilia are arranged in a definite order in rows. In the posterior half of the body the rows are nearly longitudinal, but in the anterior

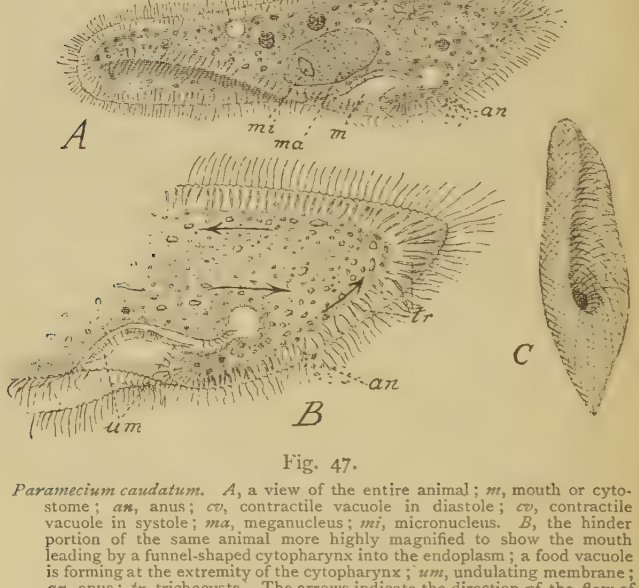

Fig. 47.

Paramecium caudatum. *A*, a view of the entire animal; *m*, mouth or cytostome; *an*, anus; *cv*, contractile vacuole in diastole; *cv'*, contractile vacuole in systole; *ma*, meganucleus; *mi*, micronucleus. *B*, the hinder portion of the same animal more highly magnified to show the mouth leading by a funnel-shaped cytopharynx into the endoplasm; a food vacuole is forming at the extremity of the cytopharynx; *um*, undulating membrane; *an*, anus; *tr*, trichocysts. The arrows indicate the direction of the flow of the granules in the endoplasm. *C*, a diagrammatic view of a Paramecium from the ventral surface, showing the mouth and peristomial groove and the striations of the cuticle. (*A* and *B*, original; *C*, after Bütschli.)

half their course is modified in connection with the spiral twist of the body, and they curve inwards towards the peristomial groove on the ventral surface. Paramecium and its near allies are placed in a group called **Holotricha**, characterised by the uniform covering of fine cilia.

The cell-protoplasm of Paramecium is differentiated into an external elastic and delicate membrane or cuticle, within this is a cortical layer (ectoplasm) of relatively dense consistency, and the centre of the body is occupied by a softer endoplasm. The cytostome, as has already been mentioned, leads by way of a short ciliated cytopharynx into the endoplasm. There is a large nucleus situated nearly in the middle of the length of the animal, and rather to one side so as to lie in the cortical layer or ectoplasm. It is called the **Meganucleus**, to distinguish it from a smaller ovoid body lying alongside of it and called the **Micronucleus**. There are two contractile vacuoles, one placed at about the end of the first quarter, the other at the end of the third quarter of the length of the body, in the ectoplasm on the dorsal side. We may now consider these structures in detail.

Examination with a very high power of the microscope shows that the cuticle is mapped out into a number of very minute hexagonal areas, from the centre of each of which a single cilium projects. These areas are slight elevations of the cuticle separated by fine grooves from one another, and they are so disposed that, under a lower magnification, the grooves appear as two sets of lines crossing each other obliquely and sweeping round towards the peristome and mouth in the manner indicated in fig. 47, *C*. (The lines are drawn much too large, for clearness sake.) Since each elevated area bears a single cilium, it is obvious that the arrangement of the cilia corresponds exactly with that of the apparent striation, and the figure therefore gives a clear idea of the manner in which the cilia are distributed over the body. It will be observed that in the region of the mouth and peristome they are arranged so as to create a current in the direction of the mouth.

The cuticle itself is not a fine homogeneous membrane or pellicle like the similarly-named structure in the Flagellata, but appears rather to be of the nature of a specialised external layer of the protoplasm in which, on the alveolar theory of protoplasmic structure, the minute alveoli are arranged side by side, so that their outer walls form a definite surface layer.

The cortical layer or ectoplasm underlying the cuticle consists of a dense semi-fluid protoplasm with a fine alveolar structure. It is relatively of considerable thickness, and contains

the more important structures of the cell-body. The two contractile vacuoles lie in the deeper part of the cortical layer and have the form and position shown in fig. 47, *A*. Each contracts with great regularity at intervals of about 10-20 seconds, the contractions of the two not being synchronous but rather alternate. Just before contraction (systole) the vacuole appears as a large clear space in the ectoplasm; in systole its walls come together and its fluid contents are expelled to the exterior, but no visible aperture for their passage can be detected. The ensuing pause, during which the vacuole is refilled with fluid, is known as the diastole. Immediately after the systole a number, varying from 6-10, of fine canals make their appearance in the ectoplasm, radiating from the spot where the vacuole disappeared by closure as the spokes radiate from the hub of a wheel. These canals may reach for some considerable distance into the surrounding cell-body, but those of one vacuole do not communicate with those of the other. The canals become swollen with fluid at their inner ends and slowly void their contents into the vacuole, which reappears, gradually filling with the fluid poured into it by the different canals till it reaches its largest dimensions, and then it suddenly contracts again. Towards the close of the diastole the different canals, having emptied their contents into the vacuole, become altogether or nearly indistinguishable.

Immediately beneath the cuticle is a layer of spindle-shaped rods lying in the most external layer of the ectoplasm. These rods are known as the **Trichocysts**. They form a tolerably uniform layer immediately below the whole surface of the cell-body, and are disposed with their long axes at right angles to the surface. Each trichocyst is about 4 μ ($\mu = \frac{1}{1000}$ millimetre) in length, is somewhat darker than the surrounding protoplasm, and betrays no sign of structure, appearing as a simple spindle-shaped homogeneous body, even under the highest powers of the microscope. But under certain circumstances they undergo a remarkable change. If a trace of acetic or osmic acid is added to the water in which a Paramecium is contained the trichocysts are suddenly projected to about eight times their former length in the form of long thread-like filaments. In the genus Paramecium the trichocysts are promptly shot out on stimulation by an irritating fluid, but those of some allied Infusoria can only be made to extend with great difficulty. As a rule the

trichocysts are only discharged at or immediately before the death of the animal, and a specimen killed for preservation is nearly always seen lying in the midst of a cloud of fine filaments formed by the exploded trichocysts. In Paramecium the exploded trichocysts are generally cast right out of the body on explosion, but sometimes they remain sticking in it by one extremity, and the animal then looks as if it were clothed with a coat of very long cilia. There is no relation, however, between cilia and trichocysts, and after the latter have been exploded, the much shorter and finer cilia can be seen between the inner ends of the trichocyst threads. Nothing is known of the mechanism by which the trichocysts are extended, and very little is known about their function. They are believed to be organs of offence and defence whereby a Paramecium seizes and paralyses its prey or defends itself against enemies. But it must be confessed that hours of patient watching fail to demonstrate that a living and actively feeding Paramecium uses its supposed weapons for capturing prey, nor does it turn them against the many living organisms which may run up against it. The trichocysts, however, are so like the thread-cells or nematocysts which are the undoubtedly offensive and defensive weapons of cœlenterates, that it is difficult to avoid the conclusion that they have a similar function.

Before entering into details about the meganucleus and micronucleus it will be well to consider the other organs. The endoplasm, occupying the centre of the body, forms by far the larger part of its bulk. There is really no sharp distinction between endoplasm and ectoplasm or cortical layer. Both have the alveolar structure characteristic of undifferentiated protoplasm, and the two pass gradually into one another, the passage being sometimes more gradual, sometimes more distinct. As a rule the endoplasm may be distinguished by the rotatory streaming movement or **cyclosis** of the granules and food particles which it contains. These may be seen to move steadily round a course which begins just above and behind the cytopharynx near the posterior end, passes forward along the dorsal side, and turns downward at the anterior extremity to return again towards the mouth on the ventral surface. This course is indicated by the arrows in fig. 47, *B*.

Whilst the ectoplasm only contains structural constituents

of the cell-body,* such as the trichocysts and the mega- and micronuclei, the substance of the endoplasm is loaded with a number of granules and particles, the products of assimilation and metabolism. The most obvious foreign substances in the endoplasm are the food-vacuoles and little balls of foreign substance taken in as food. The food-vacuoles, which, of course, must not be confounded with the contractile vacuoles, are clear spherical spaces looking like bubbles in the protoplasm, and filled sometimes with fluid only, sometimes with solid food particles surrounded by fluid. The structure and behaviour of the food-vacuoles of Paramecium are the same as those of Amœba (p. 135). Besides the food-pellets there are numerous minute crystalline particles which are probably excretory products. It has also been shown that the endoplasm of Paramecium contains diffused animal starch or glycogen, giving the characteristic port-wine red colour on treatment with iodine. Since the contents of the food-vacuoles and the food-pellets are in various stages of disintegration, and since glycogen is shown, in higher animals, to be a reserve material formed by the activity of protoplasm from the substances taken in as food, we can have no doubt that a portion at any rate of the food of Paramecium is converted into glycogen in the endoplasm, is further built up as required into the substance of the body, and that the waste materials resulting from the breaking down of the protoplasm are excreted partly by the contractile vacuoles, partly in the form of the crystalline particles found in the endoplasm. The endoplasm is clearly the seat of the digestive and to a great extent of the anabolic activities of the animal. Surrounded as it is by the firm ectoplasm and the external cuticle, solid food can only be introduced into it by means of the mouth. Paramecium feeds chiefly on minute infusoria and flagellata which are swept into the mouth by the cilia lining the peristomial groove and the entrance to the mouth itself, and it has already been shown that the cilia in these regions are so disposed as to direct the currents towards the mouth. A drawing of the mouth as seen

* An exception, however, must be made in the case of *Paramecium bursaria*, in which the green symbiotic algæ, though they are not, strictly speaking, structural constituents of the cell-body, are situated in the ectoplasm, and, when they pass into the endoplasm, are digested and served as food.

under a magnification of 1000 diameters is given in fig. 47, *B*. It commences as a wide funnel-like cavity at the posterior end of the peristomial groove. The cuticle is reflected so as to line the cavity, and the cilia are also continued into it. The mouth narrows somewhat rapidly to form a narrow ciliated tube or cytopharynx which is directed at first upward, then turns downward with a slight spiral twist and ends in the endoplasm of the posterior third of the body. The entrance to the cytopharynx is guarded by the so-called **undulating membrane.** This structure (*um.* in fig. 47) has the form of a fine transparent membrane, starting like a frill near the anterior border of the mouth and passing along its dorsal wall into the commencement of the narrow cytopharynx. The free edge of the frill hangs down into the cavity of the mouth, and its other edge is obliquely inserted in the dorsal wall of the mouth cavity. The membrane vibrates rapidly with an undulating movement, and is evidently formed from a row of fused cilia, for its free edge is often frayed in the manner shown in the drawing. The inner end of the cytopharynx is furnished with sparse and rather stout cilia, which move with a relatively slow undulating movement, recalling the ciliary action of the so-called flame-cells in the excretory organs of certain Metazoa. The ingestion of food by Paramecium may easily be studied by adding finely powdered carmine or sepia to the water in which it is contained, or very frequently, if the specimen under observation is imprisoned in freshly-made gum-arabic, it will swallow the gum. Particles may be seen to be driven into the cytostome and down the cytopharynx by the action of the cilia, their course being apparently guided by the undulating membrane. At the extremity of the cytopharynx a vacuole is gradually formed in the endoplasm in which the solid particles are accumulated: the vacuole grows larger and larger till it reaches the size represented in fig. 47, *B*. Then there is a sort of gulp, a contraction of the surrounding protoplasm, the vacuole is separated from the end of the cytopharynx and passes with its solid contents into the endoplasm, where it is at once carried away by the cyclotic current, and a new vacuole forthwith begins to form in its place.

Just as a special aperture or cytostome is required to admit of the entrance of solid food into the endoplasm, so a special exit is required for the passage of insoluble remnants of food

and solid excretory substances to the exterior. This is furnished by the so-called temporary anus or **cytoproct**, a spot situated a little way behind the mouth opening on the ventral surface. The cytoproct is not a permanent aperture, or at least it is not permanently open, and it can only be detected at the moment when excreta are being discharged through it. Then it has the appearance of a minute circular orifice placed upon a small papillary projection of the body. But as soon as the solid matter is voided the aperture and papilla vanish, and no trace of them can been seen. Whether the orifice is really temporary, and its lips fuse together after an evacuation, or whether it is permanent, and its lips are only pressed together, is a matter of conjecture.

The meganucleus and micronucleus lie just above the mouth in the ectoplasm. The meganucleus is a relatively large structure, measuring from 30-35 μ in its longer, and 15-20 μ in its shorter diameter. It has a definite nuclear membrane which, in the resting condition, appears to be filled with minutely granular contents staining deeply with the ordinary dyes. The micronucleus, in the resting condition, is a small ovoid body, measuring some to 10 μ by 7 μ, placed alongside of and close to the meganucleus. When at rest it stains less intensely than the meganucleus, but its staining capacity varies in the different phases which it goes through in the course of division.

There is good reason to suppose that the meganucleus is chiefly concerned with the nutritive, the micronucleus chiefly with the reproductive processes of the animal, and the evidence for this statement will become apparent during the description of the processes of reproduction and conjugation.

Reproduction in Paramecium is a simple process of transverse binary fission. Prior to the division of the cell-body both meganucleus and micronucleus elongate and divide, the former amitotically, the latter by a simple form of mitosis. In either case the nucleus becomes dumbbell-shaped, the chromatin passes to its extremities, until finally the two swollen ends are connected by a fine thread which presently snaps in the middle and the nuclear division is complete. At the same time a constriction divides the cell-body into two equal halves, which separate and form two new Paramecia. A swarm of Paramecia, well supplied with food in the shape of fresh hay

infusion, will continue to multiply by binary division for many generations. Careful observation has shown that a Paramecium, kept under observation in a drop of hay infusion in a moist chamber, will divide two or three times a day for some forty-eight hours, but the rate of division is reduced on the third day, and on the fourth day, when Bacteria begin to disappear from the drop, it is greatly diminished. If fresh hay infusion is not added, division ceases and the now numerous progeny of the original Paramecium show evident signs of starvation. But they will recover if supplied with more food, and continue to divide as before. Under carefully devised conditions a numerous stock of Paramecia, the descendants of a single individual, may be cultivated for a considerable length of time. But not for an indefinite period. A series of careful and long-continued experiments have shown that, if fresh hay infusion is constantly added, the stock of Paramecia will multiply at the normal rate of one or two divisions per diem, with slight variations, for the space of about three months. Then a period of depression sets in, not directly attributable to a change of temperature or any other assignable cause. In such a period the rate of division becomes slower and slower and finally ceases; many individuals die and others appear moribund. At such a crisis the survivors can be artificially stimulated to fresh activity and endowed, as it were, with a new lease of life. In one case the jolting of a railway journey was observed to have a marked effect in increasing the rate of asexual multiplication by division, but a far more effective stimulus was afforded by a change of diet. When the depressed and moribund Paramecia were fed with beef extract, they rapidly recovered and resumed their normal rate of division. After a time the revived progeny could be restored to a diet of hay infusion and continued to multiply asexually for another period of three months. Then a second period of depression set in, more profound and deadly than the first. The few survivors were with difficulty kept alive on a diet of beef extract, but after a month they had so far recovered that they were again able to maintain themselves and resume the normal rate of multiplication in hay infusion. The experiments were carried on continuously for twenty-three months, at the end of which time the last surviving descendants of the parent individual of the stock died out in the seven hundred and forty-

second generation. The final result of these very interesting and laborious experiments was to show that under certain conditions the life cycle of Paramecium exhibits periodic cycles of vigour and depression, as measured by increment or decrement in size and in the rate of multiplication by asexual reproduction. At the end of every three months there was a period of diminished vitality, but not so profound as to require more than a slight stimulus for complete recovery. At the end of every six months, however, the period of depression was profound and lasting and the stock was only maintained by the application of a strong stimulus. As time went on the six-monthly periods of depression became more and more pronounced. Beef extract failed to revive the moribund individuals, and recourse was had to extracts of brain and pancreas. Finally these stronger stimuli failed in their effects and the race died out altogether. The conclusions to be drawn from these facts are sufficiently obvious. A swarm of Paramecium is incapable of maintaining itself by asexual reproduction for an indefinite period, even when supplied with an abundance of suitable food and maintained under the most favourable conditions of temperature. At regularly recurring periods the vitality of the race diminishes, but can be restored by artificial stimulation. After a time, however, stimulation ceases to be effective, and the race dies out as a result of what, for want of a better term, we may call senile decay.

In the case of Paramecia living in a state of nature, the available food supply must vary considerably from time to time, and it can only be by the rarest coincidence that a change of diet affording the necessary stimulus is provided at the onset of a period of depression. The animalcules would therefore perish, either for want of food or because their vital energies are exhausted, if the onset of degeneration were not arrested by the natural stimulus afforded by the act of conjugation. Indeed, the experiments of which mention has been made show that conjugation is the natural means by which these organisms renew their vitality whenever a depression period sets in, for in the control cultures which were kept going alongside of the series under observation, numerous cases of conjugation were observed to synchronise with the depression periods. Prior to conjugation the individuals move hither and thither in a rapid and excited manner as if

in search of one another. After a while they come together in couples and conjugate. Two individuals become attached together mouth to mouth in such intimate union that there is actual protoplasmic continuity from one to the other. The two conjugating individuals or gametes are exactly like one another, though of small size as compared with normal free

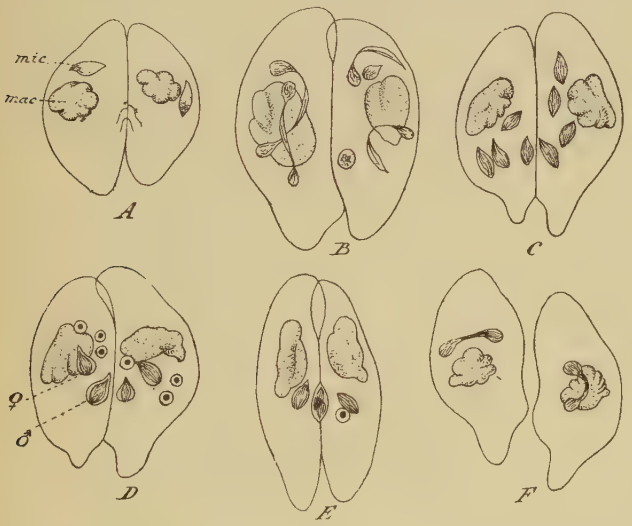

Fig. 48.

Stages in the conjugation of *Paramecium caudatum*. *A*, Stage A, the micronucleus in each gamete preparing for division. *B*, Stage B, the daughter nuclei in each gamete dividing. *C*, Four micronuclei in each gamete. *D*, Three of the four micronuclei are disintegrating; the surviving nucleus in each gamete has divided to form ♂ the male, and ♀ the female pronucleus. *E*, The male pronuclei crossing over. *F*, Conjugation effected; separation of the gametes and division of the combination nucleus. (After Maupas.)

swimming forms. The usual length of *Paramecium caudatum* is 300-325 μ, the gametes rarely exceed 210 μ in length. As a rule the process of conjugation begins during the late hours of the night, and the early hours of the morning, and lasts till late in the following afternoon. The first event following on the union of the gametes is that the micronucleus of each leaves its normal position in a cleft of the meganucleus, lies

free in the protoplasm and swells to twice its former size. This period of growth is distinguished as Stage A, and is represented in the annexed diagram (fig. 49), by the space enclosed between the lowest horizontal lines. The two next stages, B and C, are occupied by two maturation divisions of the micronucleus. This structure undergoes remarkable changes of shape: it elongates and becomes fusiform, and then doubles up to form a crescent. In the fusiform stage a granular division centre can be distinguished at one of its ends and from this a number of chromatin threads, connected at intervals by short cross junctions, run to the opposite end. In the crescent stage the division centre has travelled to the middle of the convex side of the crescent and the chromatin threads have been resolved into a number of elongated chromosomes. It seems probable that each chromosome is formed of two lengths of chromatin thread closely united side by side, for the chromosomes are observed to divide longitudinally into halves. The division centre elongates to form a spindle set at right angles to the length of the crescent, and division of the micronucleus follows, the horns of the crescent being gradually drawn in to the equator while the halves of the chromosomes travel to either pole of the spindle. This first maturation division is very possibly a meiotic division. As soon as it is completed the two daughter-micronuclei in each gamete again divide, but in this case do not form crescents but long fibrous spindles (fig. 48, *B*), the chromosomes again undergoing longitudinal division into halves in the course of the mitosis. As soon as this second maturation division is completed all the four daughter-nuclei in each gamete begin to prepare for a new division by elongating to form fibrous spindles, but only one, and it is always the micronucleus that happens to be nearest to the cytostome, passes through the further stages of mitosis and divides. The three others are arrested at the spindle stage, and then gradually degenerate and are absorbed, leaving not a trace behind. In the division of the surviving micronucleus the chromosomes split up into rows of granules lying along the course of the spindle fibres, and the granules are divided into two unequal groups by a transverse division. The smaller chromosome group passes into the male and the larger group into the female pronucleus resulting from the division. In each

gamete the smaller male pronucleus is placed close against the cytostome, the larger female pronucleus occupying a deeper position (fig. 48, *D*). Both male and female pronuclei elongate and form fibrillated spindles, and then a transference of micronuclear material is effected, the male pronucleus of one gamete passing over and fusing with the female pronucleus of the other, and *vice versâ*. The all-

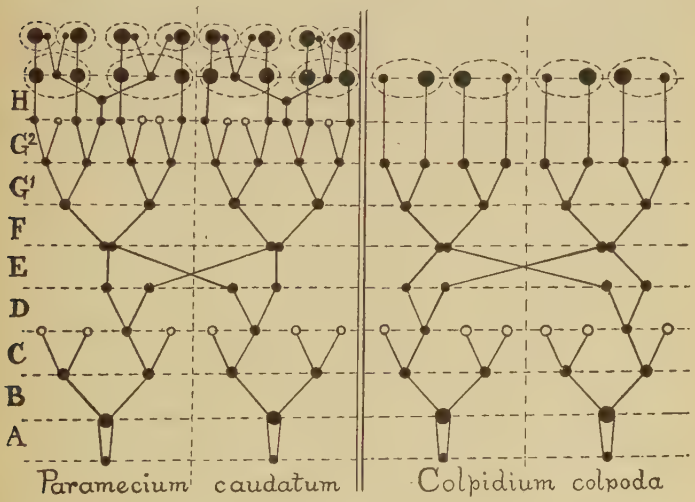

Fig. 49.

Diagrams of the course of conjugation in the two infusoria *Paramecium caudatum* and *Colpidium colpoda*. The transverse lines represent the different stages into which the process may be divided. The black circles represent persistent nuclei, the empty circles stand for those which disintegrate and disappear. The divisions of the gametes are represented by the ovals enclosing the nuclei at the top of the figure. (After Maupas.)

important act of conjugation, the transference of nuclear material, has now been effected, and the gametes, which have diminished in size during conjugation, shortly afterwards separate from one another, begin to feed again and recover their original dimensions. Each possesses the original unaltered meganucleus and a rather large micronucleus, now called the **Combination nucleus**, formed by the union of the male pronucleus of the other gamete with its own female

pronucleus. Immediately after separation the original meganucleus undergoes changes which lead to its final disappearance. It becomes deformed by the appearance of numerous folds on its surface, and at a later stage splits up into a number of irregular shreds which elongate to form long interlacing ribbons. Eventually these ribbons divide into a number of spherical corpuscles, which are either cast out of the body or incorporated with the new meganuclei subsequently formed, according as the progeny of the ex-gamete are well fed or starved. Meanwhile the combination nucleus in each ex-gamete has undergone three successive mitotic divisions (stages F, G^1 G^2 in the diagram) and there are eight products of the combination nucleus arranged in two groups of four, one group at the anterior and another at the posterior end of the body. The four nuclei of the anterior group increase in size and eventually become the meganuclei of the progeny of the ex-gamete. Of the posterior group three members atrophy and disappear, one alone surviving as a micronucleus. Some twenty-four to thirty hours after separation the ex-gamete divides in such a manner that two of the new meganuclei pass into one product of division and two into the other, whilst the micronucleus (which at this stage is not very much smaller than the meganuclei) divides mitotically, one of its products entering each of the two daughter Paramecia. A second division quickly follows, accompanied, as before, by mitotic division of the micronucleus, whilst the meganuclei are again passively distributed among the products of division. The end result is that each ex-gamete has produced four normal Paramecia containing each a meganucleus and a single micronucleus, both derived from the combination nucleus. These Paramecia feed and multiply by transverse division at the normal rate of two or three divisions in the twenty-four hours.

The course of conjugation is in all essentials the same in the other members of the genus Paramecium as in *P. caudatum*, but the details are slightly different. In *P. bursaria* the final stages are somewhat simplified, and resemble those of *Colpidium colpoda*, a ciliate infusorian whose conjugation is represented in the diagram (fig. 49) for comparison. It will be observed that the behaviour of the micronucleus up to stage G^1 is identical with that of *P. caudatum*, but that four daughter-nuclei are formed from each combination nucleus instead of

eight, and at the first division two of these become the meganuclei and two the micronuclei of the daughter forms. In *P. bursaria* the original meganucleus does not break up as it does in *P. caudatum*, and it is doubtful whether it is eventually resorbed or whether it fuses with one of the new meganuclei.

The phenomena of conjugation in *Paramecium caudatum* are worthy of most careful study, for they have been worked out more carefully in this species than in any other Protozoon, thanks chiefly to the brilliant researches of Maupas and Calkins. Comparing the course of events with those observed in other Protozoa, it will be observed that in Paramecium there is no distinction of sex as far as the two gametes are concerned. Both are exactly alike and equal in size. But there is an indication of differentiation in the micronuclear products, so that we have not hesitated to call the active product the male and the passive one the female pronucleus. Again, it is remarkable that the conjugation is only temporary, the two gametes separating and dividing, each on its own account, after the mutual transfer of micronuclear material has been effected. There is no fusion of cytoplasm, and no zygote is formed.

Perhaps the most striking result of Maupas' and Calkins' researches is the evidence, more surely founded than in the case of Polytoma or Copromonas, that in Paramecium and a large number of other ciliate infusoria there is a definite limit to the reproductive faculty, and when this limit is reached death ensues if conjugation does not intervene to restore the lost fertility. It would appear that in these lowly organised creatures there is, as in the higher animals, a period of growth, of bloom, and of decay ; that the organism wastes and wears out in the exercise of its functions, and requires rejuvenation from time to time in order that its activities may not be brought altogether to a stop. This rejuvenation is effected, in a manner unknown to us, by the act of conjugation, and Paramecium shows better than any other example, that the essential thing in conjugation is the mingling of nuclear material derived from two different individuals.

In a Protozoon like Paramecium or Polytoma there is a distinct life cycle, which comprises the alternation of a sexual or conjugate generation with a series of asexual generations reproducing their like by simple binary fission. The products

of fission of a zygote separate from one another, lead free individual existences, and form a stock or family which has a limited term of existence, for its members degenerate and die if they do not conjugate at the proper time. In a Metazoon the product of fertilisation is the fertilised ovum or oosperm, comparable to the zygote of a Protozoon. The oosperm reproduces itself, just as Protozoa reproduce themselves, by binary division, but its progeny, instead of separating, remain adherent, forming an integral whole or individual. Countless numbers of cells are formed by repeated binary division, and the whole, of which they form a part, grows into what we call the adult organism. This we may compare with the sum of the numerous individuals forming a stock or family of Protozoa. Even as the Protozoon family has a limit of existence, degenerating and eventually dying if that limit is overpassed ; so the Metazoon body, composed of the innumerable progeny of the oosperm, has its well-marked phases of growth, maturity, decay, and death. In both cases the extinction of the race is provided against by the act of conjugation or fertilisation, by means of which the forces of life—to use a vague expression—are as it were rejuvenated and started on a new cycle of activity by the commingling of the nuclear material of two simple cells. Further than this we see a close parallel in the manner in which the nuclear material is halved, before fertilisation, by the formation of the polar bodies, or by the division of the spermatocytes, in the Metazoan ovum and spermatozoon and the similar maturation divisions in Actinosphærium, Copromonas, and Paramecium. The alternation of generations, so obvious in many Protozoa, would seem to be masked in the Metazoa by the coherence and integration of the cell progeny of the fertilised ovum.

Thus the ovum and spermatozoon might be regarded as the sexual generation of cells, the tissue-cells derived from them as the numerous asexual generations, and the cycle is completed on the reappearance of the ovum and spermatozoon. Such comparisons open up a wide field of inquiry, the interest in which is further increased when one studies the parallel series of events in plants ; and the gradations exhibited by Pandorina, Eudorina, and Volvox seem to supply a real basis to speculation. But at present the whole subject is too obscure to be discussed with profit. It must not be forgotten that no pro-

cess of conjugation has yet been observed in Amœba and Euglena; and that, in Actinosphærium, the gametes are the identical pairs of so-called secondary cysts formed by the binary division of the primary cysts, modified only to the extent of their having ejected part of their nuclear matter in the form of polar bodies. Amongst so many seeming contradictions it is as yet impossible to lay the foundations of a solid theory.

Much has been said of late years of the potential immortality of Protozoa. But the facts described for Copromonas, Polytoma and Paramecium, as well as those about to be described for Vorticella, show that these creatures, like the higher forms of life, are subject to the inexorable laws of decay and death. If it should be established beyond doubt that Amœba (or any other Protozoon) is capable of multiplying itself indefinitely by binary division, without loss of functional activity calling for repair by means of conjugation, then indeed it could be said that these organisms are immortal in that decay and death would not come to them of necessity, but as an accident, through deprivation of food or violence. But we know too little of the life history of Amœba to allow of our making any positive assertion about it, and the same may be said of most other Protozoa. We must be content at present with the positive evidence afforded by the life-histories of Paramecium and allied forms, which demonstrate that the organism would wear out and perish were it not refreshed, rejuvenated from time to time, by the act of conjugation. How it is that conjugation rejuvenates the enfeebled organisation we cannot say.

But it must be remembered, whilst we admit decay and death as the natural accompaniments of existence, that the life-stuff, protoplasm in its widest sense, is immortal. All the evidence at our disposal forces us to believe that living matter can only be born from living matter. Organisms are not bred, as was once believed, from slime and mud, but only from other organisms, and all that now lives on the earth is descended from that original life-stuff whose origin will ever be a mystery to us.

CHAPTER XII

THE CILIATA (continued)—VORTICELLA

The genus which we are now going to study is very common and rich in species. Specimens may be collected during the warmer months in almost any freshwater pool or ditch, where they are generally found adhering to the stalks of water-weeds. Or one may nearly certainly obtain a cultivation of Vorticella by making an infusion of hay and dead leaves in soft water and leaving it to stand for a time. After the first stages of putrescence have passed a thick brown scum will form on the surface, and numerous specimens of Vorticella will be found adhering to the under side of this scum.

There are many species of Vorticella, differing from one another in so small a degree that it is often very difficult to identify them. The following description refers chiefly to *Vorticella monilata*, a species which frequently makes its appearance in vegetable infusions, and is easily recognisable because of the warty excrescences with which its body is studded.

In shape Vorticella may be compared to an inverted bell, with a very long handle. Imagine the rim of the bell to be thickened and beset with a circle of cilia, and its mouth to be almost closed by a discoidal plug, placed to one side so as to leave between it and the thickened rim a slit leading into the interior. Further, imagine that the handle is hollow and traversed by a contractile cord thrown into a loose spiral so that on contraction of the cord it is shortened into a close corkscrew-like spiral, and one has a very fair idea of the general appearance of the organism.

In the genus Vorticella the individuals may be closely crowded together or may stand at some little distance apart on the weed or other substance to which the stems are attached, but they are always separate and independent of one another. In the closely allied genera *Zoothamnium* and *Carchesium* the

stems are branched, and each branch bears a bell-shaped animalcule at its extremity, so that there is a colony composed of numerous individuals organically connected with one another by means of the branching stems. The bell-shaped expansion will be called the **body**, the handle the **stalk**. The contractile cord traversing the stalk is the **contractile filament**; the discoidal plug nearly filling up the orifice of the bell-shaped body is the **disc**; the groove formed between the thickened rim and the disc is the **peristomial groove**; the tube leading into the interior of the body is the **cytopharynx**, and its opening into the peristomial groove is the **cytostome**.

Having settled on these terms, we may proceed to examine the structure of the animal in detail. The first thing to be observed is the distribution of the cilia. They are not scattered over the whole body, as in Paramecium, but they are reduced to two circles or whorls, one placed on the thickened marginal rim, the other on the edge of the disc. In addition, there are cilia in the cytopharynx, and there is an undulating membrane of large size forming a sort of triangular flap, one side of which is attached along the peristome and the entrance to the cytostome. (Fig. 50, *A*, *un*.) The size and arrangement of the cilia can easily be understood by reference to the accompanying figure. Because of the restriction of the cilia to the peristomial region, Vorticella and its allies are placed in an order **Peritricha**.

The bell-shaped body consists, as in Paramecium, of cuticle, cortical layer or ectoplasm, and a soft internal endoplasm. The cuticle, like that of Paramecium, must be regarded as the surface layer of the protoplasm, in which the alveoli, because of their superficial position, assume a particular arrangement. The cuticle is variously striated or otherwise ornamented in different species. In *Vorticella monilata*, as has already been said, it is covered with closely-set warty prominences.

The ectoplasm is the layer immediately beneath and continuous with the cuticle. It exhibits the usual alveolar structure of protoplasm, and differs from the ectoplasm of Paramecium in being devoid of trichocysts. But in Vorticella one can recognise structures of which there was no trace in Paramecium—namely, a layer of very fine contractile fibres lying immediately beneath the cuticle. These fibres are not

a product of the ectoplasm, but a differentiation of the walls of the alveoli of the cuticular layer. They begin as a number of very fine and rather widely separated fibrillæ close underneath the peristomial ring, and run longitudinally down the body towards the stalk. At about one-third of the length of the body from the hinder end the cuticular layer is thickened so

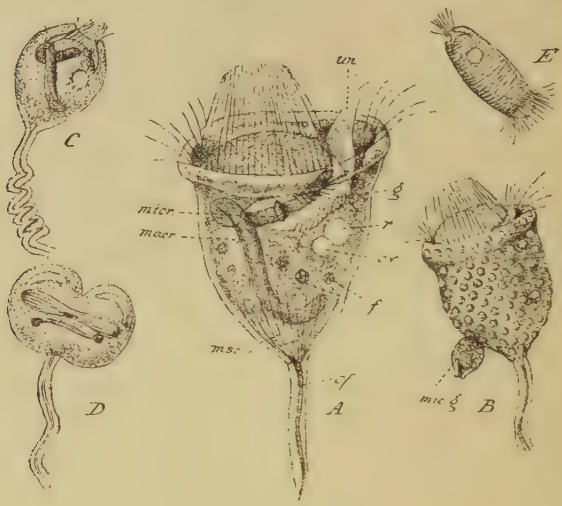

Fig. 50.

A, a specimen of *Vorticella monilata* viewed as a transparent object; *un*, undulating membrane; *g*, cytopharynx; *macr*, meganucleus; *micr*, micronucleus; *r*, reservoir; *c.v.*, contractile vacuole; *f*, food vacuoles; *msc*, muscular fibrillæ at the base; *c.f.*, contractile filament. *B*, another specimen of the same species showing the warty prominences characteristic of the species; and *mic g*, a microgamete which has just attached itself. *C*, a specimen partly retracted to show how the peristome is unfolded over the disc. *D*, a specimen dividing; the meganucleus and micronucleus drawn out into fibrillated spindles. *E*, a microgamete of V. nebulifera. (*A* to *D* original; *E* after Claparède.)

as to form a ring encircling this part of the body, and the fibrillæ appear to be attached to this ring and then to bend rather suddenly inwards, traversing the thickened ectoplasm in the hinder part of the body. Converging together, the fibrils unite where the stalk is joined to the body and are continued into it as the contractile filament. Usually the converging

fibrils at the hinder extremity of the body are easily recognisable, whilst those at the anterior end are difficult to see.

Anyone who watches a living Vorticella will easily see that the creature not only springs to and fro by the contractions of its stalk, but that it also has the power of expanding and unfolding its peristomial disc. When it is fully expanded the peristomial rim is everted, somewhat like the mouth of a bell, the disc is protruded, and the beautiful whorls of cilia situated on these organs are fully displayed. In some species the disc is protruded far above the margin of the peristome; in others, as in *V. monilata*, it hardly rises to the level of the peristomial rim.

In contraction the disc is withdrawn and the peristomial ring is contracted and folded inwards over it. The whorls of cilia are turned inwards and covered over by the enfolded margins of the peristomial rim, and the whole body assumes the shape of a pear. It has been said that the contraction of the peristome is effected by means of a circular layer of contractile fibres or sphincter lying in the peristomial ring. Such fibres may be present—one can hardly imagine how the contraction of the peristome could take place without them—but many of the best observers have failed to distinguish them, and the writer has been equally unsuccessful.

The contractile filament, formed, as has been shown, by the union of the basal contractile fibres of the disc, traverses the stalk as a homogeneous doubly refracting thread, which in the expanded condition forms a very loose spiral, in the contracted state is tightly coiled up. The filament is ensheathed in a transparent elastic tube which is not a continuation of the so-called cuticle of the body, but an ectoplastic product secreted by the posterior end of the animal, and probably of a chitinous nature. The space between this tube and the contractile filament is occupied by a transparent homogeneous mass of gelatinous consistency, and it is probably due to the presence of this substance that on contraction of the filament the whole stalk is coiled up in a spiral, and the body drawn down towards the point of attachment. The stalk being closed below, the contractile filament does not project beyond it.

Returning to the structure of the body, we find that the cytostome leads into a narrowed ciliated cytopharynx, which, in *V. monilata*, turns through a half-spiral and ends in the

endoplasm near the middle of the body. The endoplasm has much the same character as that of Paramecium, containing food-vacuoles, pellets, and granules, which move round and round in a regular cyclosis.

Close alongside of the cytopharynx is a large clear space, which is stationary and generally distinguished from the food-vacuoles by its larger size. This cavity is filled with fluid, and communicates by a very narrow passage with the cytopharynx; it is a reservoir like that already described in Euglena. Close beside it is a contractile vacuole, whose contents at every contraction are poured into the reservoir, whence they are slowly emptied into the cytopharynx, and so to the exterior.

Like Paramecium, Vorticella is in need of a special aperture for the expulsion of undigested matter and solid excreta. This aperture is situated in the cytopharynx close to the opening of the reservoir, and is known as the **cytoproct**. It is often a permanent opening with a short and narrow tube leading to the endoplasm, but these relations vary very much in different species.

A meganucleus and a micronucleus are present. The former is very large and elongated. In some species it has the form of a horseshoe, in others it is like a twisted riband. Its shape and position in *V. monilata* can be better understood from an inspection of fig. 50, than from any description. The micronucleus is small, and is placed close alongside of the meganucleus in the anterior end of the body. The micronucleus stains with great difficulty, whereas the meganucleus seizes on the ordinary dyes with great avidity and obscures all the structures lying against it. Hence the micronucleus is difficult to see, but it can usually be demonstrated in living specimens, and better still in specimens cleared in glycerine after being killed in a 10% solution of corrosive sublimate to which a few drops of acetic acid have been added.

Vorticella reproduces itself by binary longitudinal fission. The peristome is contracted, and the body becomes depressed and transversely elongated. The meganucleus is straightened and comes to lie transversely across the middle of the body, forming a fibrillated spindle like that of a Paramecium preparing for division. The micronucleus elongates to form a spindle placed alongside of the meganuclear spindle and both become dumbbell-shaped and divide. (Fig. 50, *D*.) A constriction

beginning at the peristomial end divides the body into two halves, both of which are at first attached to the same stalk. But one moiety develops an additional ring of cilia at its posterior end, this ciliated ring being always coincident in position with the thickening of the cuticle described in connection with the contractile fibrils. It then becomes detached from the stalk, swims away by means of its ciliated band, and after a time attaches itself to some object by its posterior end, forms a new stalk for itself, loses its posterior circlet of cilia, expands its peristomial field, and so develops into a new Vorticella. The other product of division remains attached to the stalk, and thus one may speak of it as the parent form, whilst the detached free swimming individual may be called the child. No such distinction was possible in the Protozoa described in the preceding pages.

Though our information on the subject is somewhat meagre there is no doubt that Vorticella is as little able to propagate itself indefinitely by binary division as Paramecium. Specimens cultivated in an organic infusion will flourish and multiply by division for three or four days, but will then dwindle and disappear if conjugation does not take place.

The conjugation of Vorticellids presents many special features which must be described in detail. It is easy enough to obtain specimens in the act of conjugating, but it is very difficult to follow out all the steps, partly because of the attachment of the creatures to foreign substances, partly because the meganucleus breaks up at an early stage into a number of minute fragments and thus obscures the micronuclei. The various steps have been followed more completely in *Vorticella monilata* than in any other species, and again we owe the most complete and accurate account to Maupas.

The gametes of Vorticella are of two kinds, **macrogametes** and **microgametes**. The former are stalked individuals differing neither in size nor in any other obvious feature from normal specimens. The microgametes, as their name implies, are much smaller, and they differ further from normal individuals in the possession of a posterior circlet of cilia. They have no stalk, but swim freely through the water by means of this accessory ciliated band.

In *V. monilata* the microgametes are formed by the binary division of an ordinary stalked form. Sometimes the products

of division may again divide, giving rise to four microgametes, but a single binary division is the rule.*

The microgametes when set free from the parent stalk swim through the water. Conjugation begins towards the hour of

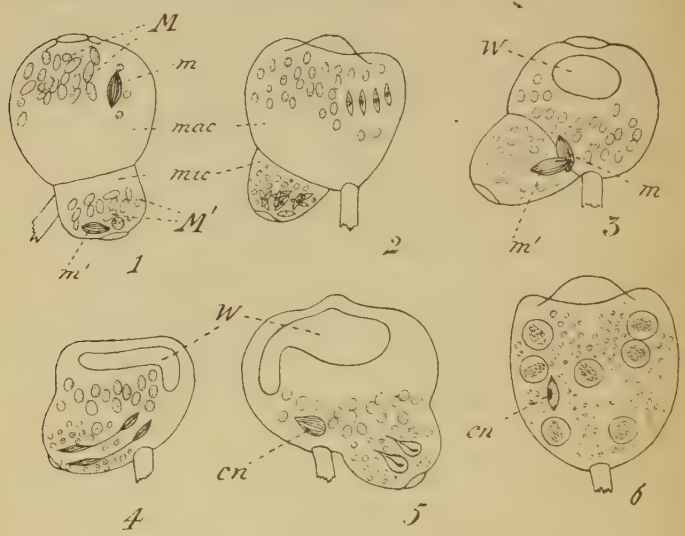

Fig. 51.

Stages in the conjugation of *Vorticella monilata*; *mac*, macrogamete; *mic*, microgamete. *M*, fragmented meganucleus of the macrogamete. *M'*, fragmented meganucleus of the microgamete. *W*, water accumulated below the peristome of the macrogamete; *m*, micronucleus of the macrogamete; *m'*, micronucleus of the microgamete; *cn*, combination nucleus. For further description see text. (After Maupas.)

daybreak and lasts from thirteen to fourteen hours. A microgamete coming into contact with a fixed macrogamete attaches itself by its posterior end to the hinder region of the body of the latter, and immediately becomes intimately fused with it. So long as it is swimming about freely the microgamete has a

* It has been so commonly stated that Vorticella gives rise by three successive binary divisions to eight microgametes that it is well to insist on the fact that Maupas has found that the microgametes are formed by equal binary division in *V. monilata*, *V. putrina*, and *V. nebulifera*; by unequal binary division in *V. microstoma*; and only by repeated binary division in the case of *Carchesium polypinum*.

single micronucleus of fusiform shape, measuring some 4·5 μ in its longer and 3 μ in its shorter diameter. Scarcely is it fixed, however, to a macrogamete, and before actual fusion has taken place, than the micronucleus undergoes mitosis and divides into two. The micronucleus of the macrogamete meanwhile remains inert. In the next stage the micronuclei are unaltered, but the microgamete loses its posterior circlet of cilia and becomes intimately fused with the macrogamete. When this is accomplished the micronuclei in both gametes increase greatly in size, become spindle-shaped, and divide by mitosis. A second division follows, and as there were two micronuclei in a microgamete and one in the macrogamete the result is that there are eight micronuclear corpuscles in the former and four in the latter. Up to this time the micronucleus of the macrogamete and its products have been situated in the anterior region of the body. The peristome being closed, water now accumulates below it and forces the four micronuclear products towards the posterior end, so that they are closely contiguous to the micronuclear corpuscles of the microgamete. Seven of the last-named then disintegrate and disappear, the one remaining moving close up against the partition which still exists between the bodies of the macrogamete and microgamete. Similarly three of the four micronuclear corpuscles of the macrogamete disappear, and the one remaining takes up a position opposite to the surviving corpuscle in the microgamete. These corpuscles increase notably in size, the dividing wall separating them disappears; they come into contact, and, on doing so, both divide mitotically. The result of the division is that one product of each micronucleus is pushed back into the body of the microgamete, there to disintegrate and be absorbed without leaving a trace. The two remaining products, constituting the male and female pronuclei, are pushed into the body of the macrogamete, where they fuse together to form a combination nucleus.

As soon as the fusion is complete the water collected beneath the peristome of macrogamete is ejected, the protoplasm moves forward to take its place, carrying with it not only the combination nucleus but also the protoplasmic contents of the microgamete. The latter is now reduced to a mere membranous appendage, which shrivels up and eventually falls off and is lost.

The combination nucleus soon elongates to form a fibrous

spindle, and divides by mitosis. Two more divisions follow, so that the macrogamete contains eight similar nuclear corpuscles. One of these does not grow any further, but assumes the characters of a micronucleus. The other seven become spherical, and grow rapidly till each consists of a central mass of granular matter separated by a clear space from a well-defined nuclear membrane. The fertilised macrogamete, if well fed, is now

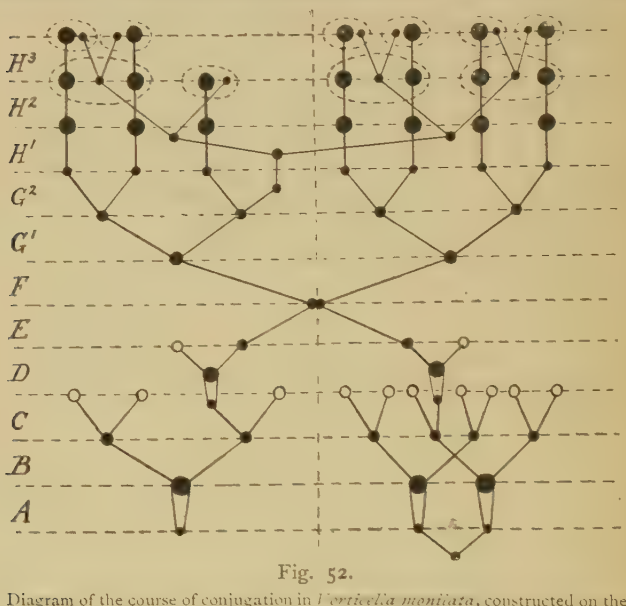

Fig. 52.

Diagram of the course of conjugation in *Vorticella monilata*, constructed on the same principle as fig. 49, which should be compared. (After Maupas.)

ready to divide. The large corpuscles, which may now be called meganuclei, do not divide, but are distributed to the offspring, four passing into one and three into the other of the two individuals resulting from the first division. The micronucleus, on the contrary, divides, one of its products passing into each of the daughter Vorticellæ. The rest of the process has not been determined with absolute certainty, but it is probable that it follows the course indicated in the diagram, fig. 52. The young Vorticellid with four meganuclei under-

goes two more divisions, each accompanied by a division of the micronucleus, whilst the meganuclei are simply distributed equally among the progeny. The young Vorticellid with three meganuclei behaves similarly, but as there are only three meganuclei to be distributed, only three young forms are produced in the manner shown in the diagram.

The fate of the original meganuclei of the two gametes has already been alluded to. At a very early stage they are broken up by abstriction into a number of fragments, those of the microgamete being always smaller than those of the macrogamete. The fragments continue to break up into smaller and smaller pieces which are finally absorbed and disappear altogether.

One cannot fail to observe that the conjugation of Vorticella is a step further advanced towards a differentiation of sex than in Paramecium. Volvox exhibits a still more marked sexual differentiation, but, whilst it is allied to animal forms, it has all the characters of a plant. Whereas in Paramecium the gametes are similar, the conjugation temporary, and both of the ex-gametes reproduce their kind, in Vorticella the gametes are dissimilar, the conjugation permanent and complete, and the resulting zygote is the sole reproductive individual. We cannot hesitate to ascribe to the active microgamete the *rôle* of the male, to the passive macrogamete the *rôle* of the female.

CHAPTER XIII

PROTOZOA AND METAZOA

When hunting for Vorticella in sea or fresh water one frequently comes across little branching colonies composed of numerous Vorticella-like individuals united together to form a sort of tree or bush. These belong to the genera *Epistylis*, *Carchesium*, and *Zoothamnium*. The genus Epistylis may readily be recognised, because the individuals forming the colony have no contractile filament and therefore cannot retract themselves by coiling their stalks. There is no organic connection between the individuals; they are merely associated together and grouped in such a way as to form a plant-like growth. In the genus Carchesium the individuals are similarly associated to form a bush-like colony, but each has a well-developed contractile filament, and can retract itself independently of its fellows. A strong stimulus may cause all the members of the colony to retract themselves at once, but generally some are retracted whilst the others remain fully extended and expanded. In the genus Zoothamnium there is a main stem with branches which again sub-divide so that the colony has something the shape of an espalier pear-tree. The contractile filament runs through the main stem, and, sub-dividing, is continued into its branches, the ultimate sub-divisions terminating in the Vorticella-like individuals. Thus all the members of the colony are organically united by means of the branched contractile filament, and a stimulus affecting any one member is immediately communicated to all the others, causing the whole colony to contract into a nearly globular form. Further than this, in certain species of Zoothamnium, the individuals of a colony are not all alike. The greater number of them, forming the termination of the twigs and branches, do not differ materially in structure from Vorticella, and measure about 0·08 mm. in diameter. Other individuals of much larger size, measuring as much as

0·12 mm. in diameter, are situated in the axils of the branches and are distinguished as the **macrogonidia**. They are globular in shape, provided with a nucleus, contractile vacuole, and a posterior circlet of cilia, but their peristomial field is permanently closed.

The arborescent form of a colony of Zoothamnium is due to the fact that longitudinal binary division of the ordinary individuals involves not only the body but also the distal half of the contractile filament, and consequently repeated binary divisions give rise to a dichotomously-branched colony. But, since both products of a division remain fixed on the branched stalk instead of one of them swimming away, there would be no provision for the foundation of new colonies unless some means were especially adapted to that end. These means are supplied by the macrogonidia, whose sole function it is to reproduce new colonies. It is not quite certain whether a macrogonidium must undergo fertilisation before it reproduces a new colony or not. At any rate it may undergo fertilisation, that is to say, it may conjugate with a microgamete. The microgametes of Zoothamnium, so far as is known, are produced by multiple division of an ordinary individual, and they have much the same appearance as the microgametes of a Vorticella. They swim away and conjugate with a macrogonidium, never with an ordinary individual. When conjugation is effected the fertilised macrogonidium is liberated from the colony, swims about for a while, and then attaches itself and divides rapidly and repeatedly, giving rise to a new colony. It also seems to be possible that a macrogonidium may be able to detach itself and give rise to a new colony without fertilisation.

An interesting comparison may be drawn between Zoothamnium and Volvox. In both these forms, though they belong to different classes of the Protista, the cell individuals formed by successive binary divisions remain in organic connection with one another and give rise to a compound organism, a stock or colony. In Volvox the cell units are so intimately connected that their individualities are to a great extent merged into the higher individuality of the stock of which they form a part, whilst in Zoothamnium the union is of a looser kind, and the individualities of the cells seem to us to preponderate over the individuality of the colony. But the difference is unimportant, the main feature in each case being the tendency

for the products of cell-division to cohere together and form a compound organism. In consequence of this coherence the reproductive faculty of the ordinary cells is limited to the increase of the bulk of the colony, and in order that the species may be perpetuated, special individuals are produced to which the function of reproducing new colonies is delegated. Thus the union of cells into a stock or colony involves, it would seem as a necessary consequence, a differentiation into two distinct kinds of individuals. The one kind, comprising what we have styled the ordinary individuals, are mainly nutritive in function and may henceforth be called the vegetative, or, better, the **somatic** cells. The other kind are almost exclusively reproductive, and may henceforth be called the **germ cells**. It should be noticed in passing that in Volvox and possibly also in Zoothamnium, the germ cells are themselves divided into separate kinds, asexual and sexual. The asexual germ cells are the parthenogonidia of Volvox and the unfertilised macrogonidia (which, if they really exist, might be called by the same name) of Zoothamnium. The sexual cells are the male and female gonidia of Volvox, the microgametes and macrogonidia of Zoothamnium.

Now it has been shown that uni-cellular organisms—in most cases at any rate—are incapable of propagating themselves indefinitely by binary division. Sooner or later they must conjugate or they will wear out and perish. What is true of uni-cellular organisms is true of the individual cells composing a colony or a multi-cellular organism. After a more or less prolonged exhibition of their vital activities they will degenerate and perish if they do not receive a fresh impulse from conjugation. But the somatic cells are incapable of conjugation; that function is limited to the male and female germ cells. Hence the union of cells to form a composite colony or individual, and their differentiation into somatic and germ cells is fraught with the inevitable consequence of decay and death for the somatic cells.

It follows that the continued propagation of a race of multicellular organisms, or cell colonies, in which there is a differentiation into somatic and germ cells, is dependent upon the germ cells, for they alone can conjugate and so rejuvenate the enfeebled powers of the organism. They are the survivors, whilst the somatic cells perish.

By following up this course of reasoning we can understand why it is that in the higher animals, the Metazoa, there is so close a connection that it amounts to identity between the processes of conjugation and reproduction.

It has been shown that in all essential respects conjugation is the same thing as fertilisation : the essential act is the mingling of nuclear material of two separate individual cells.

It has further been shown that a recurrence of conjugation (or fertilisation, which is the same thing) at no long intervals of time is essential to the maintenance of the vital activities.

If then in a cell-composite, or, as we call it, a multi-cellular individual or Metazoon, the capacity for conjugation is restricted to certain cells only—viz. to the germ cells—it becomes evident that in proportion as organisation advances from the uni-cellular to the multi-cellular condition, and from homogeneity of cell-structure to heterogeneity of cell-structure, so will the primitive distinction between reproduction and conjugation become less and less, until finally only those cells are reproductive which are capable of conjugating—namely, the ova (macrogametes) and spermatozoa (microgametes).

We learn, then, that the progress from uni-cellular to multi-cellular structure involves a division of labour amongst a community of cells, a differentiation in the first instance into somatic and germ cells. The somatic cells, incapable of conjugation, run through a certain course of vital activity and then wear out and perish. But before they perish they give rise to other cells, germ cells, which are capable of conjugation. When two of these have united, the product, a fertilised ovum, enters upon a new career of activity, divides, gives rise to a new composite of somatic cells, and the cycle is again repeated.

The steps through which this condition came to be established in the course of evolution are indicated by the series Gonium, Pandorina, Eudorina, and Volvox, and much more obscurely by the series Vorticella, Carchesium, Zoothamnium.

It is not permissible to suppose that either of these series represents the actual ancestral form of the Metazoa (see p. 214) but they enable us, with good reason, to trace the possible course of evolution from one great division of the animal kingdom to the other.

It is very probable that Protozoa developed into Metazoa, not once, but many times over, and that the classes of Metazoa

which we recognise to-day may have sprung from different uni-cellular groups. In this connection it is interesting to note that, although the Flagellata and Ciliata are distinct classes of the Protozoa, and have developed along characteristic lines, they both exhibit similar tendencies in evolution. In both we find the successive steps of simple adhesion of equivalent cells, followed by organic connection with a differentiation into vegetative and reproductive, somatic and germ cells, the series culminating in the one case in Volvox, and in the other in Zoothamnium. Volvox, however, must be ranked as a plant: and it should be noticed that the life cycle of plants is not so simple as that of animals. Plants retain the capacity of reproducing themselves asexually, as Volvox does by means of its parthenogonidia, and an alternation of asexual and sexual generations has been established, the one succeeding the other with great regularity. It is by no means certain that the macrogonidia of Zoothamnium can develop without fertilisation or, as it is said, parthenogenetically, but if they can the fact is exceptional in the animal kingdom. Some few animals, it is true, are capable of reproducing themselves parthenogenetically by means of reproductive cells which do not require fertilisation, and in them there is a more or less regular alternation of generations. But in the great majority there is no such alternation but an unbroken succession of sexual generations.

It must now be evident that although we attempt to draw a sharp distinction between the Protozoa and the Metazoa, defining the one group as uni-cellular the other as multi-cellular, the existence of the two series which we have been considering breaks down the barrier implied by our definitions. If a Metazoon is a multi-cellular organism reproducing itself asexually by ova and spermatozoa, it would be hard to say why Volvox (leaving its vegetable affinities out of the question) should not be classed among the Metazoa. It is, as a matter of fact, placed among the Protozoa because it is directly connected through Eudorina and Pandorina with the uni-cellular Flagellates, and is not similarly connected by transitional forms with any higher animal or plant. So it is simply classed amongst its nearest kinsmen. And it is obvious that, if the theory of evolution is true, and if we could recover all the animal forms which have become extinct, it would be impossible to fix the point where the Protozoa ceased and the

Metazoa began. The one group must have passed imperceptibly into the other, and it is only because the intermediate forms have become extinct that we are led to draw a hard and fast line between uni-cellular and multi-cellular organisms. And even now the Flagellata, and in a lesser degree the Ciliata, are there to remind us that our definitions are arbitrary and artificial.

But, after all, our conception of a Metazoon is not quite simply that of a multi-cellular organism, propagating itself by sexual reproduction, as will appear from the study of the animals described in the following chapters.

CHAPTER XIV

THE CŒLENTERATA—HYDRA FUSCA AND HYDRA VIRIDIS

The little fresh-water polyps, known by the generic name of **Hydra**, so common in our pools and streams, are by common consent chosen as the type of the simplest form of Metazoan structure. To depart from well-established custom and choose another type would occasion inconvenience, so custom must be adhered to in spite of the fact that Hydra is far from being as simple and primitive in structure as was at one time supposed. One of the simpler forms of sponges, abundant enough in certain localities on our coasts, would serve better as an illustration of a primitive type of multi-cellular organisation.

Two species of Hydra are abundant in streams and pools in Great Britain. The one, of a yellow or light brown colour, is known as *Hydra fusca*. The other is called *Hydra viridis* because of its bright green hue, due to the presence of innumerable green chlorophyll-containing corpuscles in its tissues. A third nearly colourless species has been recognised and named *Hydra grisea*, but it differs so little and in such unimportant characters from *Hydra fusca*, that it need not engage our attention.

Hydra fusca being selected for descriptive purposes, the general shape of the animal may be described as that of a cylindrical sac forming the body, attached by one end to water-weed or other object. At the opposite distal end the sac opens to the exterior by a small orifice, the **mouth**, situated on the top of a conical elevation termed the **hypostome**. A circlet of simple, tapering, arm-like processes springs from the junction of the hypostome with the body wall. These processes are the **tentacles**. They vary in number in different specimens, but there are seldom less than six and never more than nine or ten.

A living Hydra adheres pretty firmly by its proximal end—

often called the foot, or better, the **basal disc**—to the object to which it is attached. It is not permanently fixed, however, but can detach itself and move slowly from place to place, either

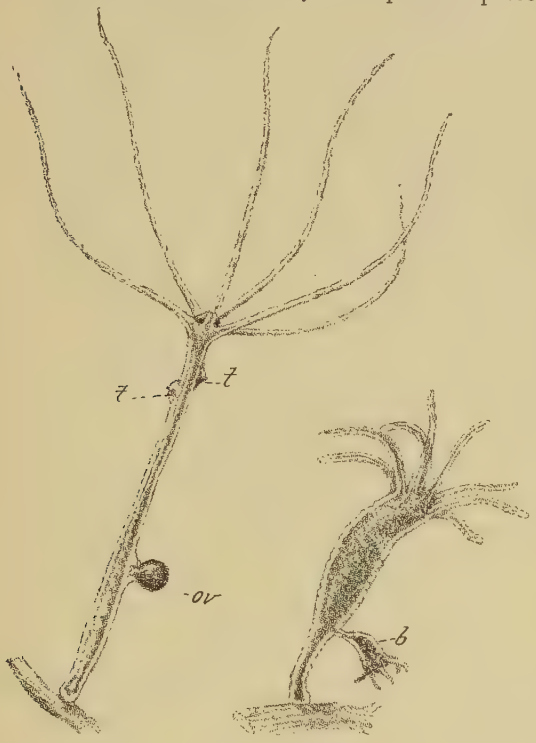

Fig. 53.

On the left hand a specimen of *Hydra fusca*, fully extended; *tt*, testes; *ov*, ovum with horny case. On the right hand a specimen of *Hydra viridis*, half extended; *b*, a bud.

creeping along by means of its tentacles, or by a series of movements resembling those of the looping caterpillar. In the latter case, the body is extended as far as possible and bent downwards till the mouth touches the weed or other object to which the animal is attached. The mouth being fixed to the

surface the basal disc is detached and drawn up, and again fixed close to the point where the mouth is attached. The mouth then lets go, the body is again extended, a fresh hold is taken by the mouth ; and so on.

A living Hydra may easily be examined in a watch-glass full of water under a simple lens or a low power of the miscroscope. After being detached it soon fixes itself again to the sides of the glass, and, if undisturbed, extends itself to a considerable length, spreading out its tentacles like a net.

Both body and tentacles are exceedingly contractile and extensible. The body of the large species of *Hydra fusca*, when fully extended, may attain a length of 7 or 8 mm. or more, whilst its diameter is reduced in proportion as its length is increased. The tentacles, when fully extended, project some 6 or 7 mm. beyond the body, and are reduced to the thickness of the finest thread. When the animal is irritated or alarmed, the body is contracted into a mere lump some 2 mm. long, and its diameter increases in proportion, whilst the tentacles are reduced to circlets of blunt finger-like projections surrounding the hypostome. All sorts of intermediate conditions between the extremes of contraction and extension may be observed. When the body is fairly extended it can be seen that the trunk is not of uniform thickness but rather club-shaped. The proximal moiety is slender and nearly colourless, corresponding to the handle of a club, whilst the distal moiety is thicker and more deeply coloured. The external difference in form corresponds with an internal differentiation of cell-structure, as will be described presently.

Hydra is carnivorous, and feeds on the "water-fleas"—*i.e.* small Crustacea, chiefly Daphnids and Copepods, which abound in fresh-water pools. If some of these organisms are placed in the watch-glass along with a Hydra, the manner in which the animal captures and swallows its prey may easily be observed. A Daphnid swimming within reach of the circle of extended tentacles is seized and held fast by them. After a short struggle it appears to be paralysed, and is drawn downward towards the mouth by the contraction of the tentacles. The hypostome being expanded and the mouth widely opened, the Daphnid is slowly swallowed and passed down into the digestive cavity. The distal moiety of the body is often swelled up by the presence of one or more water-

fleas, which have been swallowed and are undergoing digestion, but they are seldom to be seen in the proximal moiety. Crustaceans have hard chitinous exoskeletons which cannot be digested. These and other indigestible matter are afterwards expelled by the mouth.

The general structure of Hydra can be studied by subjecting the animal to slight pressure under a cover-glass and examining it under a moderate power of the microscope; but in order to study details one must have recourse to very thin longitudinal and transverse sections and to the method of maceration. By the first method of examination it can be seen that the body is a simple sac, having a single spacious internal cavity, the **gastro-vascular cavity**, whose walls are formed of two layers of cells separated by a fine membrane. The external layer of cells, forming the outside skin of the body and tentacles, is colourless, not very thick, and studded, especially on the distal moiety of the body and on the tentacles, with numerous small ovoid capsules, the **nematocysts**. This outer layer is known as the **ectoderm**. The inner layer, or **endoderm**, is notably thicker, and is full of granules and small brown corpuscles which render it opaque. The colour both of *H. fusca* and *H. viridis* is due to the brown or green corpuscles contained in the endoderm cells, and the distinction between the colourless ectoderm and the endoderm stuffed full of green corpuscles is particularly well marked in the latter species.

Between ectoderm and endoderm is a very thin layer of colourless gelatinoid material, distinguishable as a transparent line in optical section. This is the jelly, or **mesoglœa**, very scantily developed in Hydra, but attaining great thickness and forming the greater part of the bulk of the body in many Cœlenterates. It is not formed of cells as the ectoderm and endoderm are, but is formed as a secretion of (probably) both of these layers.

The general structure of the tentacles is the same as that of the body. They are simply hollow processes of the latter, each containing a prolongation of the gastro-vascular cavity, bounded by the two cellular layers ectoderm and endoderm, with the mesoglœa between. When retracted a tentacle is thick and bluntly finger-shaped, its surface thrown into a number of coarse transverse wrinkles. When fully extended it is attenuated and filiform, the wrinkles disappear, and the

surface is covered by a number of warty projections beset with minute stiff hair-like projections. Further examination shows

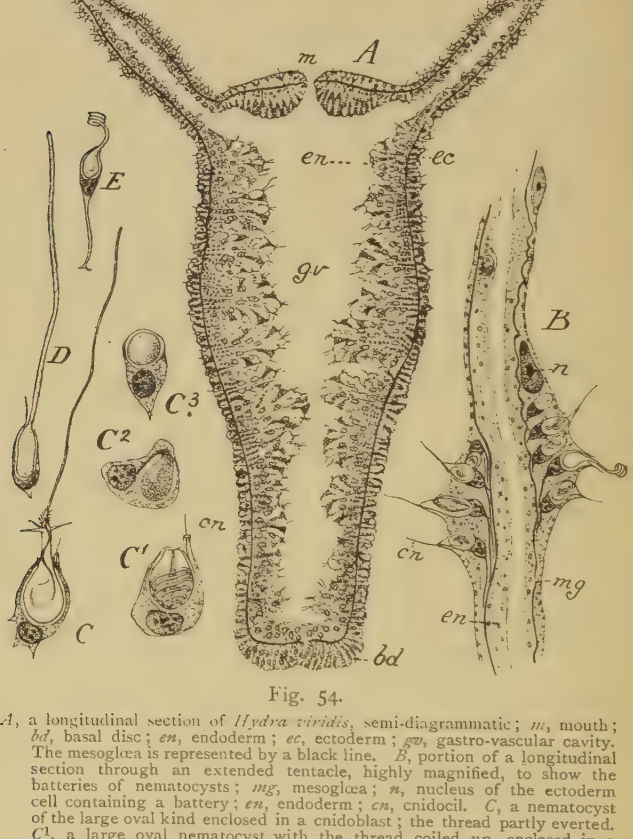

Fig. 54.

A, a longitudinal section of *Hydra viridis*, semi-diagrammatic; *m*, mouth; *bd*, basal disc; *en*, endoderm; *ec*, ectoderm; *gv*, gastro-vascular cavity. The mesoglœa is represented by a black line. *B*, portion of a longitudinal section through an extended tentacle, highly magnified, to show the batteries of nematocysts; *mg*, mesoglœa; *n*, nucleus of the ectoderm cell containing a battery; *en*, endoderm; *cn*, cnidocil. *C*, a nematocyst of the large oval kind enclosed in a cnidoblast; the thread partly everted. C^1, a large oval nematocyst with the thread coiled up, enclosed in a cnidoblast; *cn*, cnidocil. C^2, C^3, stages in the development of a nematocyst. *D*, an elongate oval nematocyst, showing the short relatively thick thread everted. *E*, a small oval nematocyst with everted coiled up thread; the cnidoblast is produced below into a long contractile process.

that each warty prominence is a lump of protoplasm, a single ectoderm cell, in fact, in which a number of highly refringent

oval and cylindrical capsules are embedded. These capsules are the **nematocysts**, organs of offence and defence possessed by all members of the phylum Cœlenterata to which Hydra belongs. The stiff hair-like processes projecting from the surface are called **cnidocils**, and it is easy to determine that each nematocyst has a single cnidocil associated with it. If a drop of acetic acid or magenta is run under the coverslip some of the nematocysts will be shot out and will assume the forms shown in fig. 54, *C*, *D*, and *E*. There are three kinds of nematocysts, the largest having the form of a pear-shaped sac, the narrow end of which is produced into a short tapering tube which narrows rapidly to form a long thread or filament. The base of the filament is armed with three stiff projecting spines and a number of smaller spines. The two other kinds of nematocysts have shorter and thicker threads destitute of spines, and the threads are usually curled up into a close cork-screw-like spiral. Before the application of the stimulus the thread in each nematocyst was introverted and coiled up inside the cavity of the sac. To understand the meaning of "introversion" the reader should imagine an india-rubber sac prolonged at one end into a closed tube. If a thread were passed up the inside of the tube and fastened to its inside at the tip, by pulling on the thread the whole tube could be drawn back into the cavity of the sac. If, then, the sac being closed and filled with fluid, pressure was exerted on its walls, the introverted tube would, in consequence of the pressure transmitted to it, be everted and thrown out sharply to its original length. There is no internal thread in a nematocyst but in other respects its structure resembles that of the imaginary india-rubber ball and tube. The contents of a nematocyst sac, however, do not appear to contain a fluid but a semi-solid gelatinoid material which stains deeply with hæmatoxylin and many other dyes. This substance is hygroscopic, and it is due to the absorption of water by it that the pressure inside the sac is increased and the thread ejected. Hydra is able to sting and paralyse its prey by means of its nematocysts, and it is probable from the paralysing effects observed in the case of the water-flea that these structures contain a poisonous secretion in their sacs.

It is clear, from what has preceded, that the structural plan, the architecture of Hydra, is of the simplest kind. It is an elongated sac closed at one end and open at the other. The

walls of the sac are formed of two distinct cell layers cemented together, as it were, by an intermediate structureless substance, the mesoglœa. An imaginary line drawn through the mouth to the centre of the surface of attachment marks out the longitudinal axis of the body. The tentacles are disposed radially with regard to this axis. There is a single internal cavity communicating with the exterior only by the mouth, and this cavity is at once the receptacle of food, the organ of digestion, and the means whereby the products of digestion are distributed. This structural plan, exhibited in its simplest form in Hydra, is diagnostic of the Cœlenterata, but is variously modified and disguised in the different classes into which that phylum is divided. Particular attention should be given to the fact that there are only two primary cell layers, ectoderm and endoderm, in the cœlenterate body, and that these correspond with the outermost and innermost germ-layers—the epiblast and hypoblast of the frog's embryo. The third middle layer, or mesoblast, is entirely absent in Cœlenterates (for the mesoglœa is not a cellular layer), and hence these animals are sometimes distinguished as **diploblastic** or two-layered animals. The name Cœlenterata calls attention to the important characteristic of a single internal cavity which, from its fulfilling the functions of digestive and circulatory systems, is called the gastro-vascular cavity.

Careful microscopical examination of the ectoderm and endoderm shows that these two layers are differentiated so as to perform various functions which in the higher three-layered animals are performed by the mesoblast. Both ectoderm and endoderm, being layers of cells spread over external or internal surfaces, come under the definition of epithelia (p. 80). The ectoderm, covering the outside of the body, is essentially the protective and sensory layer; the endoderm, lining the internal cavity, is essentially the digestive and secretory layer. The two layers become continuous with one another at the lips of the mouth.

Partly because of their delicacy, partly because of the intimate union of their component cells, the tissues of Hydra are very difficult to study. Two methods are available. The animal may be killed and hardened by plunging it suddenly in a mixture of acetic acid and corrosive sublimate, or, preferably, in the mixture of chromic, osmic, and acetic acids, known

as Flemming's fluid. It is then embedded in paraffin, cut into very thin sections with a microtome, and stained. A combination of borax-carmine, and picro-nigrosin following corrosive sublimate, or safranin and light green following Flemming's fluid, gives the best results. But in either case the action of the reagents and the paraffin has such a destructive effect on the tissues that many of the finer details are lost.

The second method is that of isolation. The animal is placed from five to ten minutes in a very weak mixture of osmic and acetic acids,* and, after being washed for a minute in distilled water, is placed for a least 24 hours in a mixture of equal parts of dilute glycerine and Ranvier's picro-carmine. It is then carefully removed and placed on a glass slide in a fresh drop of dilute glycerine. Slight shaking suffices to separate the cells from one another, or, if they still adhere, the layers may be stripped off with a fine hair mounted in a pen-holder. The coverslip should be put on cautiously and supported by a hair. If the preparation is successful, the individual cells will come apart and can be very satisfactorily studied, as they are stained by the picro-carmine.

The ectoderm differs in structure in the tentacles, basal disc, and body wall. That of the body wall will be described first. Each cell is somewhat the shape of an inverted cone, the broad end external and the narrow internal end produced into a tapering process which rests upon, or rather is continued into, one or more contractile fibres placed at right angles to the long axis of the cell. (Fig. 55, *A*.) The contractile fibre is as much as ·38 mm. long, and lies close against the surface of the mesoglœa parallel to the long axis of the animal's body. It is invested throughout its length by a fine coat of protoplasm, continuous with the protoplasm of the body of the cell. The protoplasmic investment is raised into a number of little prominences, and so looks jagged and indented on its lower surface. The body of the cell is composed of coarsely alveolar protoplasm, the alveolar walls forming a reticulum of denser substance, which, in the lower moiety of the cell, is drawn out into a network of fibrils which may be traced into a connection with the basal

* Schneider recommends the following mixture: A ·02 % solution of osmic acid, 1 part. A 5 % solution of acetic acid, 4 parts. This mixture gives good results, but macerates rapidly. The tissues should not be left in it longer than four minutes.

contractile fibre. A large nucleus, with a distinct nucleolus (sometimes there are two nucleoli) and a network of very fine chromatin particles, occupies the middle of the cell. The external moieties of adjacent cells are fused together by intimate union of their protoplasmic walls, hence it is very difficult to isolate a single cell, and if one is isolated its edges look torn and jagged, as is shown in the outermost cells in fig. 55, *A*.

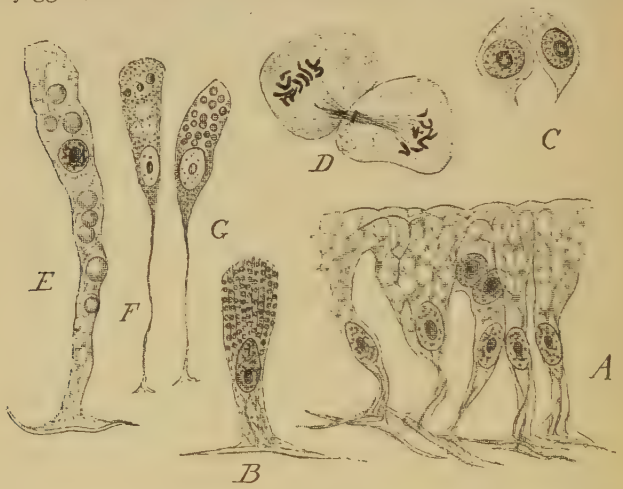

Fig. 55.

Isolated cells from *Hydra fusca*. *A*, a group of ectoderm cells from the body wall showing the muscular fibres. *B*, an ectoderm cell from the basal disc showing the secretory granules. *C*, two interstitial cells from the ectoderm. *D*, an interstitial cell dividing, very highly magnified. *E*, an endoderm cell, not very highly vacuolated, with muscular process, nucleus, and plastids. *F* and *G*, two forms of gland cell from the endoderm of the body wall.

The cells are limited externally by a cuticle which, under the highest powers of the microscope, is seen to contain a number of minute refringent particles. When the animal is fully extended the cuticle forms a continuous even layer over the surface. When it is contracted, and its walls are thrown into furrows and wrinkles, the cuticle dips down into the valleys between the wrinkles. To sum up, the ectoderm of Hydra is mainly composed of columnar epithelial cells, differing from an ordinary epithelium chiefly in the fact that each cell has formed

at its base one or more long contractile muscular fibres. Each cell, then, partaking of the characters of an epithelial and an unstriped muscular cell, is called an **epithelio-muscular cell.** It should be borne in mind that the muscle fibres are relatively very long, and that therefore they extend upwards and downwards among the similar muscle-fibres of adjacent cells, forming a regular longitudinal layer of muscle-fibres closely applied to the mesoglœa.

The other elements of the ectoderm of the body wall are the sub-epithelial or **interstitial** cells and the nematocyst-forming cells or **cnidoblasts.** As the epithelio-muscular cells taper towards their bases spaces are left between them which in the distal moiety of the body wall are occupied by numerous round or cubical cells, each having a nucleus with a nucleolus. Their nuclei are considerably smaller than those of the epithelio-muscular cells. These rounded cells may be called indifferent, because they are as yet undifferentiated and are destined to give rise to other elements, cnidoblasts and sexual cells. Frequently they may be seen in active division, and their products may be observed to develop into cnidoblasts or into ova or spermatozoa. The majority go to form cnidoblasts. A nematocyst, whether of the large oval, cylindrical or small oval kind, is always the product of a single cell, and is formed inside that cell. In the upper part of the body wall one can see nematocysts in all stages of growth. First a clear space appears in an interstitial cell; this space enlarges, it acquires a definite wall, and its contents stain deeply. Presently it elongates, and one end is produced to form the thread, which at its first appearance is everted and coiled round the outside of the sac. After a time the thread is introverted—it is not quite clear how—and the nematocyst assumes its final form. When nearly ripe a nematocyst, still contained in its mother-cell or cnidoblast, migrates *into the inside* of an epithelio-muscular cell and approaches the surface. The external end of the cnidoblast is produced to form a cnidocil which perforates the cuticle, and the gun is, so to speak, loaded and cocked, ready to explode on the pressure of the trigger—the cnidocil. It is a most remarkable thing that, whilst nematocysts occur in all parts of the ectoderm, with the exception of the basal disc, and especially in the tentacles, the developing stages of nematocysts are almost exclusively confined to the

distal moiety of the body wall, where the indifferent interstitial cells are most abundant. The exploded nematocysts of the tentacles must be renewed, and since they are not formed *in situ*, they can only be replaced by the new capsules formed in the distal region of the body wall. How this replacement is effected is not known. It can only be by migration of the cnidoblasts, but the fact of migration has not been satisfactorily established, though as it has been shown that the outer moieties of the epithelio-muscular cells are confluent and form a practically continous sheet of protoplasm, there appears to be no obstacle to migration.

In the late spring and summer months, when Hydra reproduces itself sexually, the indifferent interstitial cells at certain defined spots multiply rapidly by division and form masses of germ cells bulging out the ectoderm. Their further development will be described later on.

Observation of a living Hydra has shown that it is highly irritable. Irritation of the tentacles will generally cause the whole animal to contract. This would seem to imply the existence of a mechanism whereby impulses generated at one part of the body may be conducted to all other parts and cause the muscle-fibres of the epithelio-muscular cells to contract in unison. In short, it would seem to imply the existence of a nervous system. It is impossible to find a trace of a nervous system in sections. Nor has the writer been able, after numerous attempts with the aid of the most approved methods of isolation, to demonstrate the existence of structures which could unhesitatingly be called nerve-fibres or nerve ganglion-cells. It is extremely doubtful whether any differentiated nervous elements occur in Hydra, but a nervous system has been described in the form of a sub-epithelial network of branching cells whose processes form a layer of varying thickness lying close on the muscle-fibres in all parts of the body. Some of the branches are said to run upwards between the epithelio-muscular cells and end in or upon them; others to make a similar connection with the cnidoblasts. These nerve cells are said to be found between the lower ends of the endoderm as well as the ectoderm cells, and to be so abundant on the hypostome as to form an ill-defined nerve ring near the bases of the tentacles.

The ectoderm of the tentacles consists almost exclusively

of epithelio-muscular cells: they are large, rather flat, and provided with several longitudinally-disposed muscle-fibres. When the tentacle is contracted each cell is transversely elongated and bulged outwards, giving rise to the transverse wrinkles already noted. When the tentacle is extended the central part of each cell forms a projecting lump, whilst its periphery is thinned out to a thin protoplasmic layer. The central lump contains a large nucleus with a distinct nucleolus, and a variable number, often as many as twelve, of nematocysts embedded in the cell substance. Usually there is one —sometimes two or three—large oval nematocyst occupying the centre of the swelling, and around this are several of the two other kinds of nematocysts—viz. cylindrical and small oval. The arrangement can best be understood by an examination of fig. 54, *B*. It will be noticed that each nematocyst is contained in a cnidoblast which is itself embedded in the epithelio-muscular cell. Each cnidoblast is furnished with a cnidocil projecting through the cuticle, the cnidocils of the cylindrical and small oval nematocysts being longer than those of the large oval form. The cell-bodies of the smaller cnidoblasts are produced internally into a fibril which, on reaching the mesoglœa, bends sharply and runs backwards amongst the muscle-fibres. The large cnidoblasts have shorter and less conspicuous fibres. There can be little doubt that these fibres are contractile, and belong to the same category as the muscular processes of the epithelio-muscular cells.

The ectoderm of the basal disc consists almost entirely of columnar epithelio-muscular cells which are filled with small refringent granules and have no external cuticle. A few interstitial cells may be found among their bases, but no nematocysts. A single cell from the basal disc is shown in fig. 55, *B*. Its outer half is longitudinally fibrillated and along each fibril is arranged a row of bright refringent corpuscles which are the secretum of the cell. Thus the basal cells are glandular as well as epithelial and muscular. Their function is to secrete a sticky substance by means of which the animal can adhere to a foreign body. Occasionally the basal cells send out pseudopodial projections from their free surfaces, and possibly the animal is able to effect slight changes of position by means of these pseudopodia.

The endoderm lines the whole of the gastro-vascular cavity,

including the cavities of the tentacles, and consists primarily of two kinds of cells, epithelio-muscular digestive cells and secretory cells devoid of muscular processes.

The character of the endoderm differs in different regions of the body. In the tentacles it consists wholly of much-vacuolated epithelial cells which are prismatic and columnar when the tentacles are retracted, flattened and elongate-oval in section when the tentacles are extended. Each cell contains a single large nucleus with a conspicuous nucleolus, and, in addition, a number of rounded corpuscles and granules. The round corpuscles in *H. fusca* are yellow in colour; they stain tolerably deeply with certain dyes but do not show any trace of internal structure. They are specialised protoplasmic structures, capable of multiplying by division, and are connected in some way unknown to us with the metabolism of the cell. In *Hydra viridis* the corpuscles are very numerous and bright green in colour. Each consists of a central protoplasmic body containing one or more clear spaces with a minute central corpuscle, which resembles a nucleolus not only in appearance but also in the fact that it stains very brightly with certain dyes. The central body is covered by an envelope of a somewhat different protoplasmic substance containing chlorophyll. The envelope is sometimes continuous, sometimes in the form of two or three cap-like plates. The whole corpuscle recalls the chromatophors found in so many Protozoa, and may be called by the same name. Experiments have shown that *Hydra viridis* is able to decompose carbonic acid in sunlight, setting free bubbles of oxygen gas. It is not known in what form the carbon is assimilated, for if an animal which has been exposed for several hours to bright sunlight is killed, placed in spirit to dissolve out the chlorophyll, and treated with iodine, no trace of starch can be discovered either in the chromatophors or in the endoderm cells in which they are contained.

A single nutritive endoderm cell from the body of *H. fusca* is shown on fig. 55, *E*. It is an elongate claviform epithelio-muscular cell containing a large nucleus with a nucleolus and a number of granules and corpuscles of different kinds. Some of these are yellow plastids, others are spherical balls made up of a number of highly-refringent angular brown particles, probably products of metabolism. After a meal such a cell will

be loaded with bright yellow glistening globules, evidently of a fatty nature, for they blacken with osmic acid. The endoderm cells lining the proximal moiety of the gastro-vascular cavity, and, in a starving Hydra, all the endoderm cells, are vacuolated to such an extent that the protoplasm is reduced to a mere envelope forming the outside of the cell and a loose network around the nucleus. The internal free end of the cell, turned towards the gastro-vascular cavity, has no cuticle, and the naked protoplasm often sends pseudopodial processes into the cavity. Normally each cell bears a pair of fairly long flagella, whose lashing movements may be observed in a transparent living specimen subjected to pressure. It seems probable that the flagella can be withdrawn and pseudopodia protruded in their place, but nothing is certainly known on this head. At its outer end, abutting on the mesoglœa, the nutritive cell widens out suddenly and gives rise to a muscular fibre resembling in all respects that of an ectodermic cell, except that it is shorter, rather finer, and disposed transversely to the long axis of the body. Hence whilst the ectodermic fibres form a longitudinal, the endodermic fibres form a circular muscular coat. The endoderm cells of the tentacles do not appear to have muscular fibres.

A nutritive cell of *H. viridis* would be exactly the same as the one described except that the yellow plastids would be replaced by much more numerous chromatophors.

The endoderm cells are closely packed together, leaving room for only a very few interstitial cells between their basal ends. Being wider at their free ends than at their bases, they are packed in bunches which look fan-shaped in section, as is shown in the diagram fig. 54, *A*. When the animal is contracted the endoderm cells are much elongated and the bunches, separated by deep valleys, project far into the gastro-vascular cavity. When the animal is extended the cells are correspondingly stretched out, the valleys become shallow, and the whole endoderm has the appearance of a rather irregular columnar epithelium.

The gland-cells are absent from the endoderm of the tentacles and basal disc; present, but in scanty number, in the proximal region of the body; abundant in the distal region, and very abundant in the hypostome. Two forms of gland-cell are shown in fig. 55, *F* and *G*. Both have a wine-glass-shaped

body, the broader end turned towards the gastro-vascular cavity, the opposite end tapering to form a fine filament which runs between the nutritive endoderm cells and is inserted by a slight basal swelling on the mesoglœa. Near the thinner end of the wine-glass-shaped body is a nucleus similar to, but smaller than the nuclei of the digestive cells. In the one kind of gland-cell the body consists of dark finely-alveolar protoplasm containing numerous minute granules and occasionally a few larger globules. In the other kind, the free end of the cell—*i.e.* the end nearest the gastro-vascular cavity—consists of large vacuoles separated by thin walls of transparent protoplasm, and each vacuole is filled with a globule of highly-refringent substance, the secretum of the cell. It is probable that the finely-granular cells are simply transitional stages of the coarsely-granular kind, which have discharged their secretion and are forming a fresh supply.

The tissues of a water-flea swallowed by Hydra are rapidly dissolved by the action of the secretion poured out by the gland-cells, and if a Hydra is killed whilst this process of digestion is going on, the nutritive cells are seen to be loaded with the products of digestion in the form of globules of a proteid and fatty nature. There is also evidence that the nutritive cells have the power of seizing solid particles by their pseudopodia and ingesting them after the manner of an Amœba. If finely-divided carmine is injected into the gastro-vascular cavity, the endoderm is soon afterwards found to be full of minute granules of carmine, generally aggregated in the form of little balls and enclosed in a vacuole. Very frequently, also, nematocysts are found embedded in the endoderm cells. Usually they are somewhat shrunken and altered in appearance as if acted upon by the digestive secretions of the cells, and three or four are often rolled together in a ball and contained in a large vacuole. Most probably these nematocysts have been swallowed with the food and ingested by the endoderm cells, to be afterwards ejected with other indigestible matters. There is no evidence that nematocysts are formed in the endoderm.

Hydra multiplies itself in two ways—asexually, by means of buds, and sexually, by the development of fertilised ova. In budding the animal gives rise to a new individual very much as a plant gives rise to a new shoot. At a spot about half-way

between the mouth and basal disc the ectoderm becomes thickened by a proliferation of its interstitial cells, and then all three layers, ectoderm, mesoglœa, and endoderm, are bulged outwards to form a hollow projection from the surface. The hollow projection enlarges to form a conical outgrowth, at the distal end of which a ring of small knobs, the rudiments of the future tentacles, make their appearance. The tentacles enlarge, a mouth is formed in their midst, and the outgrowth has assumed the shape of a small Hydra whose tissues and gastro-vascular cavity are continued into those of the parent form. Several such buds may be formed at one time on a single Hydra, and some of them may give rise by a similar process to secondary buds, so that a little composite stock or colony of Hydræ is produced, all having their gastro-vascular cavities in communication with that of the parent. Sooner or later, however, the buds drop off and lead independent existences as free individual Hydræ. It should be noticed that the method of reproduction by budding, whilst undoubtedly asexual, differs from the asexual method of reproduction observed in Volvox and described as characteristic of the majority of plants. In the latter case a single cell is produced which, without previous fertilisation, segments and develops into a new organism. In budding, the tissues of the parent pass over into the like tissues of the offspring, ectoderm into ectoderm and endoderm into endoderm.

The summer months appear to be the season of sexual reproduction for *Hydra viridis*, October and November for *H. fusca*, but specimens bearing reproductive organs are never very abundant. As a rule, both male and female organs are produced by the same individual: hence Hydra is said to be hermaphrodite or **monœcious**. But several authors have described broods of Hydra which produced either exclusively male or exclusively female organs, so Hydra may be said to be occasionally **diœcious**.*

The gonads, whether male or female, may easily be distinguished from rudimentary buds by the fact that the latter always contain a central fold of coloured endoderm, the former never. The ovaries, of which there is generally only one, but occasionally several, are developed at the upper end of the

* **μόνος**, single; **δίς**, twice; **οἶκος**, a house.

posterior third of the body. The testes, generally two or three and frequently more in number, are borne on the upper third of the body wall, rarely extending down to the middle and posterior thirds.

An ovary originates as an ectodermic swelling caused by the rapid multiplication of indifferent interstitial cells. In this manner a mass of primitive ova or oogonia is formed, but of these only one undergoes further development and becomes an oocyte. (See p. 117.) The remainder are arrested in growth and go to form food material for the oocyte, which increases greatly in size, takes up a central position amongst its fellows, and begins to emit pseudopodial processes. As it grows it seizes upon and ingests the arrested oogonia as an Amœba ingests its prey, storing up their digested products in the form of a number of dark spherical corpuscles, which have been called pseudocells, but which we had better call yolk corpuscles or **deutoplasts**. Whilst these processes are going on—they last for several days—the ectoderm cells in the neighbourhood of the developing ovary swell up and form a covering for the oocyte and the oogonia or reserve cells on which it feeds. By the time that all the reserve cells are eaten up, the ovum has increased enormously in size and the ectoderm cells covering it are stretched till they form only a thin envelope around it. The ovum withdraws its pseudopodia, assumes a hemispherical shape, and by two successive unequal divisions gives rise to two polar bodies. Whilst these are being formed a structureless gelatinoid substance is secreted between the ovum and its covering cells. After the formation of the polar bodies the ovum becomes quite spherical except for a flattened area where it rests upon the mesogloea. The covering cells become very thin, break at the distal pole of the ovum, and shrink backwards towards its base, leaving its protoplasm naked except for an envelope of the gelatinoid material secreted at the previous stage. (Fig. 56, *A*.) The ovum is now ready for fertilisation, which is effected in the normal manner, by the entrance of a single spermatozoon.

A testis originates in the same way as an ovary—viz. as a proliferation of indifferent interstitial cells of the ectoderm giving rise to a little mass of germ cells—spermatogonia. The mass is enclosed by several epithelio-muscular covering cells, whose expanded outer ends form the wall of the testis, their

elongated bodies forming columns which traverse the mass of spermatogonia and imperfectly divide it up into compartments. The spermatogonia develop into spermatocytes, and each spermatocyte divides to form four spermatids, which develop directly into spermatozoa. (See p. 118.) A spermatozoon of Hydra has a conical head, consisting almost entirely of nuclear matter, a small protoplasmic middle-piece, and a fairly long vibratile flagellum.

After fertilisation, the ovum divides, still remaining attached by a short stalk or foot to the parent. The segmentation is total and regular. Two successive meridional divisions divide the ovum into blastomeres, and the next equatorial division produces an eight-celled stage. At this period, a space—the segmentation cavity or blastocœle—appears between the inner ends of the blastomeres. The final result of segmentation is a hollow sphere or **blastula**, having a wall composed of a single layer of cells surrounding a central cavity, the **blastocœle.** (Fig. 56, *B.*)

It is a striking fact that in two animals so far apart in the animal scale as the frog and Hydra the result of segmentation is the same—viz. the formation of a blastula.

The next step is the formation of a two-layered embryo, which is effected in Hydra by a process known as **multipolar immigration.** During the growth of the blastula the planes of division of the blastomeres were radial, but now several of the cells undergo tangential divisions and the innermost of their products pass into the blastocœle. Other cells, again, slip bodily from their position in the blastula wall and pass into the blastocœle, and eventually the latter cavity is completely filled up by cells which have been derived by these two methods from the blastula wall. Immediately after this the outermost layer of cells—*i.e.* those of the blastula wall—divide rapidly by radial divisions and form a definite layer of columnar epithelium sharply marked off from the inner mass of cells. (Fig. 56, *D*, *ec.*) This outer layer may now be called the ectoderm, the inner mass the endoderm.

All this while the embryo remains attached to the parent and has no external protection save the thin gelatinoid coat described above. The ectoderm cells now secrete a thick external chitinous envelope covered all over with thorny processes, and one result of their activity is that the deutoplasts

Fig. 56.

Development of Hydra. *A*, the ovum filled with deutoplasts; *ec*, ectoderm of the parent Hydra; *mg*, mesoglœa; *en*, endoderm; *B*, blastula stage, in which some cells of the blastula wall are passing in towards the interior; *blc*, segmentation cavity or blastocœle. *C*, the blastocœle nearly filled up by immigrant cells. *D*, an embryo further developed with *sh*, an external spiny, and *shi*, an internal protective envelope; *ec*, ectoderm; *i*, inner solid mass of cells. *E*, the embryo still enclosed in its double protective case, flattening itself out. *F*, the embryo creeping out of its protective envelopes; lettering as in *A* and *D*. *G*, the empty envelope after escape of the embryo. (*D*, original; the rest after Brauer.)

which they contained are absorbed and disappear. The endoderm cells are still full of deutoplasts, and so the two layers are still more sharply marked off from one another. After the thick chitinous shell is formed, a second thin, homogeneous elastic envelope is formed within it, and about this time the embryo is detached from the parent and falls to the bottom. It is now a solid aggregate of cells, divided into an outer layer with finely granular protoplasm, and an inner mass stuffed with reserve material in the form of deutoplasts. The whole is enclosed by two protective envelopes. In this condition the embryo passes into a resting stage and undergoes no change for several weeks. The first sign of further development is the appearance of a number of small rounded cells between the inner ends of the ectoderm cells. These are the interstitial cells. There is as yet no trace of a mesoglœa. A further resting period follows the development of the interstitial cells, and then the embryo, which has hitherto been subspherical, takes the form of an egg, the smaller end turned upwards, the broader resting on the bottom. The shell cracks and its upper half comes away in pieces, allowing the embryo to push the smaller end of its body out into the water.

The embryo is now more transparent than heretofore; the ectoderm and endoderm are well defined, and the mesoglœa is established as a boundary between them. A clear space, the beginning of the gastro-vascular cavity, makes its appearance in the endoderm of the emergent upper half of the body, and this space gradually extends, probably as a result of the disintegration of the central cells of the endodermic mass, to the lower end. As the embryo protrudes itself further from the shell its upper end expands and the tentacles are formed as a ring of small hollow outgrowths. The mouth is formed as a split in the centre of the ring of tentacles, placing the gastro-vascular cavity in communication with the exterior. The young Hydra is now complete. It creeps out of the half of the shell in which it has up till now been seated, attaches itself to some other object and enters upon its adult career.

CHAPTER XV

OBELIA GENICULATA

Everybody who has been to the seaside in the summer months is familiar with the large jelly-fishes which often float in millions past the shores. But everybody is not so familiar with the much smaller transparent jelly-fishes, measuring some 3 mm. in diameter, which really are more abundant. They can easily be caught in a fine muslin net towed slowly behind a boat, and they are beautiful little objects when turned into a glass jar or aquarium. So unlike is one of these little jelly-fishes, or **Medusæ**, to a Hydra, that nobody would suspect that it is at once the child and the parent of a hydra-like form, yet such is the case as the present chapter will show.

The organism known as *Obelia geniculata* is a little stock or colony formed by the repeated budding of a Hydra-like person produced from the ovum. We have seen in the last chapter how Hydra gives rise to lateral buds, and that sometimes these may produce secondary buds before they drop off from the parent stem. Now if a Hydra were to grow to a considerable length and produce a single bud which did not drop off but lengthened out and in turn produced another bud, and if this secondary bud produced a tertiary and the tertiary a quaternary, and so on, a simple colony of hydriform persons would result, all of whose members would be united together and have their gastro-vascular cavities in connection. This condition is realised in Obelia. There are several species in the genus differing from one another chiefly in their mode of budding, and consequently in the eventual form of the plant-like colonies which result from budding. The species known as *Obelia geniculata* is at once the simplest and most common of the genus. It is to be found in great abundance just below low-water mark, generally growing on the broad fronds

of the oar-weed (Laminaria). A portion of a colony is shown in fig. 57, *A*. The colony consists of a root-like branching

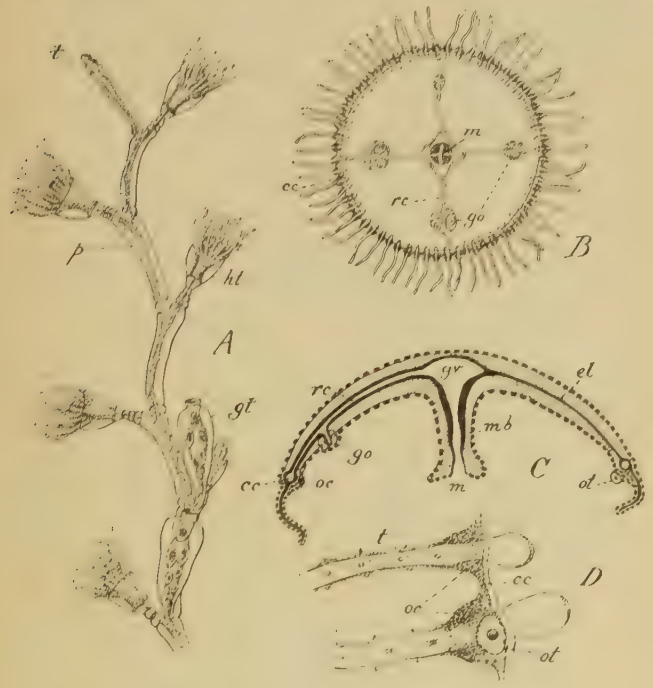

Fig. 57.

A, part of a colony of *Obelia geniculata* magnified; *ht*, hydrotheca containing a hydranth; *gt*, a gonotheca enclosing a blastostyle with medusa buds; *p*, perisarc; *t*, terminal growing point. *B*, a sexually mature female medusa, seen from below; *m*, mouth; *rc*, radial canal; *cc*, circular or ring canal; *go*, gonads. *C*, diagrammatic longitudinal section through a medusa; *m*, mouth; *mb*, manubrium; *gv*, gastro-vascular cavity; *rc*, radial canal; *cc*, ring canal; *el*, endoderm lamella; *oc*, ocellus; *ot*, otocyst. The section is supposed to pass through a radial canal on the left side and an adradial tentacle on the right. Endoderm black; mesoglœa shaded; ectoderm represented by a broken line. *D*, the bases of two tentacles magnified, showing *oc*, ocelli; *ot*, an otocyst on an adradial tentacle; *cc*, ring canal.

stem, the **hydrorhiza**, which adheres to the oar-weed and sends off at frequent intervals little branches some 10 to

20 mm. in height. Each branch consists of a somewhat zig-zag axis, the **hydrocaulus**, which at every bend gives off a very short ringed branch ending in a little terminal polype which, from its resemblance to a flower, is called a hydra-flower or **Hydranth**. The hydrocaulus and its branches consist of a delicate tube with a triple wall of ectoderm, mesogloea, and endoderm protected externally by a relatively stout but transparent chitinous investment, the **perisarc**. The soft tissues do not fill the cavity of the perisarc, but are bound to it at intervals by processes of the ectoderm cells. At every joint the perisarc is ringed, as shown in the figure, and the little branchlets which bear the hydranths are made up of three or four such rings. At the base of each hydranth the perisarc is expanded to form a pretty vase-like cup, known as the hydra-case or **hydrotheca**, into which the hydranth can be withdrawn.

An individual hydranth does not differ very much in structure from a Hydra, but its cell-elements are smaller and in some particulars simpler. The tentacles are numerous, twenty-eight to thirty in number, arranged in a single circle, and they differ from those of Hydra in being solid instead of hollow, the axis of each being occupied by a single row of large discoid endoderm cells with stout walls of cartilaginoid consistency. The interior of each of these cells is greatly vacuolated, the protoplasm being reduced to a little column surrounding the nucleus placed in the centre of the cell, and a few radiating strands. The ectoderm is thin, but loaded with nematocysts at the extremity of each tentacle.

The hypostome is enormous, forming a sort of ante-chamber to the gastro-vascular cavity, and the endoderm lining it is richly supplied with gland-cells. Further details may be learned from an inspection of fig. 58. The proximal part of the hydranth is flat and rests upon a sort of shelf near the bottom of the hydrotheca. The centre of this shelf is perforated by the neck of the hydranth or **hydrocope**, very narrow at first, but soon swelling up to pass into the hydrocaulus. A glance at the figures shows that the cavities of all the hydranths communicate with the cavity of the hydrocaulus, and so with one another.

The hydranths are solely nutritive persons. Their function is to catch, swallow, and digest prey, and, since they are all

in communication, there is a community of nutrition among the members of the colony. But a hydranth has nothing

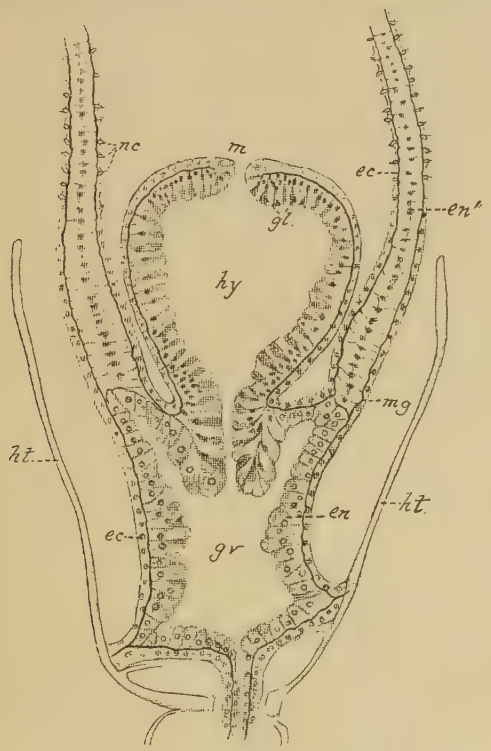

Fig. 58.

Longitudinal section through a hydranth of *Obelia geniculata*; *m*, mouth; *hy*, placed in the cavity of the hypostome; *gv*, gastro-vascular cavity; *ec*, ectoderm; *en*, endoderm; *mg*, mesoglœa; *nc*, nematocysts on the tentacles; *en'*, large vacuolated endoderm of the solid tentacle; *ht*, hydrotheca.

to do with reproduction, except that it gives rise to a bud in prolongation of the colony. (For it must be understood that although the apparent stem and flowers are called by different names they are not organically different structures.

The hydranth itself only represents the upper end of a polype the rest of whose body consists of the section of the hydrocaulus between it and the hydranth next following.) When the colony has attained to a certain size special reproductive persons are formed as buds in the axils of the branches—*i.e.* in the angles between the hydranths and the hydrocaulus. These buds give rise to tubular outgrowths called **blastostyles,** each blastostyle being nothing more than a degenerate hydriform person without mouth and tentacles. It is enclosed in a special investment of the perisarc called a **gonotheca** ; that of *Obelia geniculata* is shaped like a Greek urn. The gonotheca and blastostyle together are sometimes called a **gonangium**. A large number of buds is formed on the sides of the blastostyle, and these, developing in a peculiar manner, give rise to Medusæ, which are set free and escape from the terminal aperture of the gonangium into the water, there to swim about as independent persons.

The Medusa-person of Obelia is shaped like an umbrella with a very short thick handle. It is quite transparent, and its structure can easily be made out without dissection. The upper convex surface of the umbrella is called the **ex-umbrella** ; the lower concave surface the **sub-umbrella** ; the handle the **manubrium**. The margin of the umbrella is fringed with tentacles, whose number varies according to the age of the medusa. At the time of liberation from sixteen to twenty-four are present in the medusa of *O. geniculata*, and as growth proceeds, the number is increased by the development of new tentacles between those already existing.

At the extremity of the manubrium is a cross-shaped opening, the **mouth**, leading into a large gastro-vascular cavity occupying the whole extent of the manubrium. This cavity is covered in above by the central part of the dome of the umbrella, but it gives off peripherally four **radial gastro-vascular canals** which run at right angles to one another through the substance of the umbrella and communicate with a **ring canal** running all round its margin. The four radial canals coincide in direction with the four arms of the cruciform mouth and define the principal secondary or radial axes of the medusa. As is the case in all the Cœlenterata, the primary or chief axis of the body is defined by an imaginary line passing through the mouth and the centre of the dome of the umbrella. The

secondary axes are disposed radially with regard to the chief axis, and we may recognise: (1) The **perradial** axes defined by the four radial canals. At the extremity of each canal is a tentacle, the base of which is swollen and covered by a thickened patch of ectoderm containing pigment and nervous cells. These patches are supposed to be sensitive to light, and are called **ocelli**. (2) The **interradial** axes are defined by four imaginary straight lines bisecting the angles formed by the perradii. At the end of every such imaginary line is found an interradial tentacle having an ocellus at its base. (3) The **adradial** axes are defined by eight imaginary lines bisecting the angles between the interradii and perradii. At the end of each adradius is a tentacle having not only an ocellus but also a little hollow vesicle containing calcareous concretions at its base. The walls of this vesicle are formed by modified ectoderm cells having fine hairs projecting from their inner ends into the cavity of the vesicle. As these vesicles are analogous to structures found in the auditory organs of higher animals, the function of hearing has been ascribed to them, and they have therefore been called otocysts. It is, however, much more probable that they are organs of balance and not of hearing, and they are more appropriately called **statocysts**. The perradial, interradial, and adradial tentacles are always developed at the time the medusa is liberated from its blastostyle; and even before that time, and always during subsequent growth, new cycles of tentacles are formed, one in each interspace between tentacles already existing. These newly-added tentacles have ocelli but not statocysts at their bases. In Obelia, then, every tentacle has an ocellus at its base, but only eight—namely, the adradials—have statocysts in addition to ocelli. The presence of statocysts on the margin of the umbrella is characteristic of the group of Hydromedusæ known as *Leptomedusæ*. In the closely-allied *Anthomedusæ* ocelli are always present, statocysts never.

Fig. 57, *C*, is a diagrammatic representation of a median longitudinal section through the medusa of Obelia. It will be seen that the bulk of the umbrella is made up by the greatly thickened jelly or mesoglœa. The ex-umbrella, sub-umbrella, and manubrium are clothed externally by ectoderm, which passes into the endoderm at the lips of the mouth. The endoderm lining the cavity of the manubrium is thick, and

composed of columnar nutritive cells, and numerous gland-cells, but it is reduced to a layer of simple cubical cells in the radial and ring canals. The diagram shows a feature which is of importance in enabling a comparison to be established between the structure of a medusa and that of an ordinary

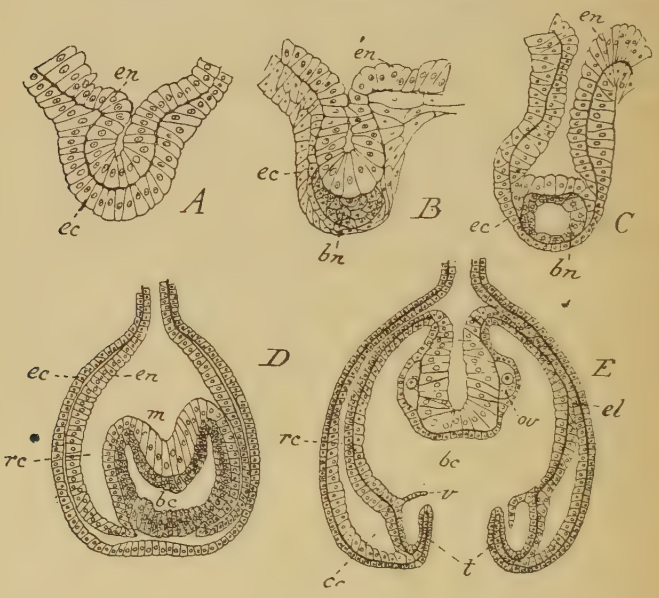

Fig. 59.

Development of the medusa in *Podocoryne carnea*, a Hydroid allied to Obelia; *ec*, ectoderm; *en*, endoderm; *bn*, bell nucleus; *rc*, radial canal; *cc*, ring canal; *bc*, sub-umbrellar cavity; *m*, manubrium; *el*, endoderm lamella; *t*, tentacles; *v*, velum, a circular curtain running round the mouth of the bell, not developed in the medusa of Obelia; *ov*, ova developing on the wall of the manubrium. For further description of the figures see text.

Hydroid polype. The section is represented as being slightly oblique, so that on the left side of the picture it passes through a radial canal, but on the right side it passes through the solid substance of the umbrella. It can be seen that the mesoglœa is traversed by a thin sheet of solid endoderm continuous centrally with the endoderm of the manubrium and peripherally

with the endoderm of the ring canal. This sheet, known as the **endoderm lamella**, extends right round the medusa, and the radial canals and ring canal are nothing more than channels hollowed out in it. These relations will perhaps be better understood after a consideration of the development of a medusa as a bud on the blastostyle as represented by the diagrams, fig. 59, *A-E*. In *A* the bud is shown as a simple hollow outgrowth of the blastostyle wall. In *B* the ectoderm cells at the extremity of the bud have multiplied and separated into *ec*, an external epithelial layer continuous with the rest of the ectoderm, and *bn*, a solid mass of cells pressed close against the sac-like outgrowth of the endoderm. This solid mass of cells is known as the **bell-nucleus**. In *C* the bell-nucleus has increased in size, and a cavity has appeared in its centre. As a consequence of its increase the centre of the endodermic outgrowth has been further pushed in, whilst its periphery embraces the bell-nucleus, so that the latter structure lies like a ball in the mouth of a double-walled cup of endoderm. In the next figure *D* the cavity of the bell-nucleus has increased greatly in size, and the ectoderm cells surrounding it have arranged themselves as an epithelial layer against the mesoglœa covering the walls of the endodermic cup. The last-named has correspondingly increased in size, and forms a deep cup with double walls. The space between the double walls is a part of the gastro-vascular cavity, and is still in free communication with the cavity of the blastostyle. A further structure has made its appearance at the bottom of the cup in the shape of a simple finger-like outgrowth of endoderm pushing before it the mesoglœa and the ectoderm of the bell-nucleus. The essential parts of the medusa are now established. The cavity of the bell-nucleus is the sub-umbrellar cavity. The walls of the endodermic cup, appearing as two horns in longitudinal section, are the endoderm lamella, still double, and enclosing a cavity reaching all round the walls of the bell or umbrella. The outgrowth at the bottom of the cup is the primordium of the manubrium. In the next figure *E* the medusa is nearly complete. The tissues at the extremity of the bud have thinned out and finally broken through, converting the cavity of the bell-nucleus into the sub-umbrellar cavity. The manubrium has increased in size, and projects freely into the sub-umbrellar cavity; a mouth will be formed at its extremity.

The double walls of the endoderm lamella have fused together over the greater part of the umbrella, but remain separate at its margin and also in four radially disposed lines reaching from the margin to the manubrium. Thus the ring canal and radial canals are the relics of a space which has elsewhere been obliterated by the fusion of the endodermic walls containing it. The first four tentacles are formed as outgrowths of the margin of the umbrella at the ends of the four radial canals; the four interradial tentacles are next formed and then the eight adradials. The medusa is now complete, but still attached by a short pedicle to the blastostyle. The cavity in this pedicle is obliterated, the pedicle breaks across and the medusa is set free: it escapes through the mouth of the gonotheca, and propels itself through the water by the rhythmical contractions of the umbrella.

We are now in a position to make a comparison between the structure of a medusa and that of an ordinary hydranth. Imagine a hydranth, like that shown in fig. 58, to have its body compressed in the longitudinal axis, and the margins to which the tentacles are attached to be pulled out so as to form a shallow cup. Then it is clear that the body will correspond to the umbrella of a medusa, the hypostome to the manubrium, and the tentacles of the flattened hydranth to the marginal tentacles of a medusa. Furthermore, it is clear that the gastro-vascular cavity of the compressed hydranth corresponds to the gastro-vascular cavity of a developing medusa, and that identity will be established by the fusion of the two layers of endoderm, excepting in the regions of the ring canal and radial canals, and by a great increase in the thickness of the mesoglœa. The hydranth and the medusa, much as they seem to differ from one another, are therefore built upon the same plan, and their several organs are homologous. But the free swimming medusa differs from the sessile Hydranth in its greater histological differentiation. In the latter there are epithelio-muscular ectoderm cells like those of Hydra. In the medusa such cells occur on the sub-umbrella, but at the margins of the umbrella and on the tentacles a more complete division of labour is often established. Part of the ectoderm cells take up a deeper situation and give rise to a layer of muscle-cells, the body of the cell being almost entirely used up in

forming a long fusiform contractile fibre resembling the unstriped muscle-fibre described in the frog, but differing from it in exhibiting a faint transverse striation. The rest of the ectoderm cells form an epithelial layer lying over the muscular layer. Further, the nervous system is better developed in the medusa than in the hydranth, consisting in the former of a ring of branched ganglion cells running round the margin of the umbrella near the bases of the tentacles and a number of scattered ganglion cells lying close upon the muscular layer of the sub-umbrellar surface, their branched processes inosculating with one another and with processes of the ganglion cells of the marginal ring.

The free medusa is the sexual member of the hydroid colony. At the time of its liberation it shows no trace of reproductive organs, but after a while a finger-like down-growth, involving both ectoderm and endoderm, is developed on each of the four radial canals. The reproductive organs are formed on the walls of these down-growths. In *Obelia geniculata* the generative cells, oogonia or spermatogonia, originate in the ectoderm of the manubrium, migrate into the endoderm, pass along the radial canals to the down-growths, and there go through the early stages of their maturation whilst still in the endoderm, but in the later stages they lie between the ectoderm and mesoglœa. The medusæ are dicœcious, ova being developed in one individual and spermatozoa in another. When the ova and spermatozoa have arrived at maturity they are dehisced into the water by rupture of the walls of the gonads, and, as medusæ float together in crowds near the surface of the sea, some of the spermatozoa are sure to come in contact with the ova to which, indeed, they are attracted as it were by a strong chemical affinity (chemiotaxis). The ovum, after fertilisation, divides and forms a hollow blastula like that of Hydra. The further steps of development have not been followed out in the case of *Obelia geniculata*, but are well known in an allied species, *Clytia flavidula*. In this species the blastocœle is filled up, as in Hydra, by immigration of cells from the blastula wall. But whereas in Hydra the immigrating cells are derived from all parts of the blastula wall, it is stated that in *Clytia flavidula* they are derived from one pole only, so that we have a process which very nearly resembles gastru-

lation—*i.e.* the folding of one half of a hollow blastula into the other half so as to produce a two-layered sac or gastrula opening to the exterior by a single aperture called the blastopore. But in Clytia there is no blastopore. The result of immigration is a solid embryo, having an external layer of columnar cells forming an ectoderm and an internal solid mass representing an endoderm. This embryo elongates and becomes pear-shaped and the ectoderm cells acquire a covering of cilia. In this stage it is known as a **planula**, a larval form very characteristic of the majority of Cœlenterata but not found in Hydra. The planula swims about for some time by means of its cilia, and during its free existence a split appears in the central mass of endoderm cells, forming the first rudiment of the gastro-vascular cavity. After a time it settles down by its broader end on some convenient submarine object, throws off its coat of cilia and begins to grow into a hydriform person, the founder of a new colony. The surface of attachment spreads out to form a disc clinging to the weed or stone to which it is fastened, and the edges of the disc soon become divided up into lobes which grow out and form the branches of the root-like hydrorhiza. The embryo elongates, its distal portion swells into a club shape, it loses its coat of cilia and the gastro-vascular cavity enlarges whilst the endoderm cells take on the characters of the adult endodermic epithelium. A mouth is soon formed at the distal extremity, a circlet of tentacles grows out round the mouth, and a chitinous tube, the perisarc, is secreted by the ectoderm. The first hydra person is now complete. It soon gives off a bud, and by continued repetition of the budding process a new colony is formed ready to go through the same life cycle as that just described.

A life-history as complicated as that of Obelia presents many problems for consideration. In the foregoing description, by calling the different members of the colony by the name of "persons" it has been tacitly assumed that they are really individuals, which have only become secondarily united to form a composite organism. And indeed one kind of person, the medusa, displays a high degree of individuality inasmuch as it leads a free and separate existence. But why are the other members of the stock or colony to be regarded as individuals united together rather than as analogues of the

members—the leaves and flowers—of a plant? Clearly because of the conditions which obtain in Hydra. When we see a Hydra bearing one or more buds we do not regard the aggregate as an individual body having members, because we know that, if we watch it long enough, we shall see the buds drop off and lead independent existences. Therefore we ascribe individuality to the buds, even whilst they are attached to the parent form. Nor, if a hydra-bud were accidentally to remain in permanent connection with its parent, should we hesitate to call it an individual and to regard the united Hydra as a compound organism, a sort of Siamese twin made up of two individuals joined together? But if this reasoning holds good for Hydra it clearly holds good for all hydroid colonies on which buds are produced in the same manner as in Hydra. Therefore the members of a hydroid stock, hydranths, blastostyles, and medusæ (as well as those other kinds of members which are found in allied genera, such as the defensive persons in Hydractinia), are regarded as individuals, and, since they differ in kind, the colony formed by their union is called **Polymorphic**.

Now, reproduction or generation means simply this, that one individual gives rise to another individual. Budding, such as occurs in the Hydromedusæ, is therefore an act of reproduction; and, as it is an asexual form of reproduction, there is an alternation of generations, an indefinite number of asexual generations alternating with a sexual generation, represented in Obelia by the medusa.

This line of argument is universally adopted by zoologists. It seems unexceptionable, but it has this result, that what they mean by alternation of generations is something quite different to what botanists mean by the same term. In plants the asexual generation or sporophyte produces reproductive cells or spores, each of which is capable, without fertilisation, of giving rise to a new organism. This new organism is not the same as the parent sporophyte, but a different form called the gametophyte, producing reproductive cells of two kinds, ova and spermatozoa, which are not by themselves able to give rise to a new organism. But if the two kinds conjugate, the product of their fusion, the oosperm, is capable of reproduction, and gives rise not to the parent gametophyte but to the sporophyte. Thus there is a regular

alternation of sporophyte and gametophyte generations such as is not found in any animal. At the same time either the sporophyte or gametophyte generation (more rarely both) in a plant is capable of vegetative multiplication of its members, multiplication being effected by a process of budding analogous to that of the Hydroid stocks. And in many plants members produced by vegetative multiplication may be detached from the parent and grow into independent organisms just as the buds of a Hydra are detached and grow into independent Hydræ. Now, the process of budding in Hydra and Obelia is clearly a process of vegetative multiplication, and it is quite open to us to consider a composite stock resulting from this process as an individual body of which the so-called persons, the hydranths, blastostyles, and medusa, are the members, just as the parts of a plant, the leaves and floral organs, are regarded as the members of the individual plant body. On such a view the medusæ set free from a Hydroid stock would be regarded as the analogues of the gemmæ and bulbils set free from so many plants, and we should apply the term "individual" not to the various members of the stock but to the whole aggregate of members, whether united or detached, which have been produced by the continued growth of the fertilised egg. In this case it would not be possible to speak of an alternation of generations in Obelia and its allies; for it would be absurd to speak of a part of an individual as a generation: and if we limit the term individual to the totality produced from the egg, and consider, as we must, that "individual" and "generation" are convertible terms, then there is only one generation in Obelia, and that a sexual one.

Whilst zoologists still hold to the opinion that a hydroid colony is a composite made up of many individuals joined together, and therefore is polymorphic and exhibits alternation of generations, it is by no means clear that the opposite view of the individuality of the so-called colony is not preferable. It is certainly more consistent with the conclusions arrived at by a discussion of the theory of individuality. It is not possible here to enter into the very complicated arguments arising out of the question, What is an individual? But the only answer which does not quickly land us in contradictions and absurdities is the one given by the late Professor Huxley—viz. that "the individual animal is the sum of the phenomena

presented by a single life : in other words, it is all those animal forms taken together which proceed from a single egg." Since all the hydranths, blastostyles, and medusæ which make up or are derived from a colony of Obelia proceed from a single egg, they comprise one individual ; there is only one generation, and consequently there can be no alternation of generations in this or any similar Hydromedusan organism.

CHAPTER XVI

ON CLASSIFICATION

Hydra and Obelia both belong to the same class, Hydromedusæ, of the phylum Cœlenterata. A cœlenterate animal is radially symmetrical with a mouth opening into a single gastro-vascular cavity serving alike for digestion and circulation ; its body wall is formed by the two primary cell layers, ectoderm and endoderm, and between these is a layer, more or less thick, of a jelly-like substance, the mesoglœa. In the Hydromedusæ the mouth opens directly into the gastro-vascular cavity, and the latter is not complicated by the presence of partitions, ridges, or filaments in its interior. The other classes of the Cœlenterata are the **Scyphozoa**, the **Anthozoa**, and the **Ctenophora**. The large jelly-fishes which abound in our seas in the warm months belong to the Scyphozoa. In this class the medusa is the dominant phase in the life-history of the organism, and the gastro-vascular cavity is furnished with gastral ridges or gastral filaments. Anthozoa comprise the sea-anemones and corals. In them the mouth does not open directly into the gastro-vascular cavity, but into a short tube lined by ectoderm which hangs down in and opens below into it. The gastro-vascular cavity is further complicated by the presence of a number of radial partitions called mesenteries passing from its walls very nearly to its centre. The Ctenophora are transparent marine animals which swim through the water by the united action of a number of comb-like plates of cilia. In structure and development they differ a good deal from other Cœlenterata, and must be regarded as an aberrant offshoot of the phylum. Amongst other peculiarities they do not possess nematocysts, but are provided instead with peculiar adhesive structures known as lasso-cells.

In the accepted system of classification a **phylum** is divided into **classes** ; a class into **orders** ; an order into **sub-orders**, and these into **families** ; a family into **genera** ; and a genus into

species. This system of classification and the nomenclature universally used was invented by the great Swedish naturalist, Carl Linnæus, in the eighteenth century. Before his time there was no system for naming animals, and no recognised subordination of groups into which animals could be placed according to their affinities. Zoology and Botany alike were in confusion, and no progress was possible. The classes, orders, and families established by Linnæus were arbitrary and artificial, and have been replaced by new groupings as naturalists came to recognise more and more clearly the natural affinities between different animals. But the system of nomenclature introduced by Linnæus still is and probably always will be in use. The system consists in giving every animal a christian name and a surname. The surname is the name of the genus to which the animal belongs, and, in accordance with the practice of the Latin language, it is put first. The christian name is the name of the species, and it is generally a trivial name alluding to some small peculiarity of the species, or it may commemorate the name of a naturalist or may be altogether fanciful. Thus *Obelia* is the name of the genus, *geniculata* is the name of the species, given to it because it is bent at every joint like a knee (Latin *genu*, a knee). A family is a group of closely-allied genera, and is usually named after one of the characteristic genera included in it. Thus the genus Obelia belongs to the family Campanularidæ, called after the genus Campanularia closely allied to Obelia. An order is a group of closely-related families, and a class is a group of closely-related orders. This methodical arrangement of groups subordinate to groups has obvious advantages: it assists the memory, enables us to take a general survey of the animal kingdom, and tells us at a glance what animals are more closely and what more distantly related to one another.

But the beginner should not forget that a modern system of classification, in which animals are arranged like the divisions, brigades, battalions, and companies of an army, aims at much more than a mere methodical grouping for the sake of precision and convenience. A good classification attempts to arrange animals as far as is possible according to their blood relationships; in other words, to group them like the branches of a genealogical tree. To use a homely illustration, a genus may be compared to a number of human

families related to one another in the first degree of cousinship. A zoological family may be compared to groups of first cousins related to one another in more distant degrees of cousinship. An order, again, to groups of distant cousins related by remoter ties of tribal kinship. A class may be compared to a number of tribes forming a nation, and a phylum to a number of nations forming a great race, like the Aryan or Mongolian race. The complete genealogy of a tribe would show the descent of all the families composing it from a common ancestor, the founder of that tribe, and it would show also the various degrees of kinship not only between the surviving families of the tribe but between all the families existing at any given time in the past. Similarly, the complete genealogy of a zoological order would show the descent of all the species contained in it from a common ancestor, and would show the degrees of kinship of all existing species and of all pre-existing species at any given period of time. But it need hardly be said that such a complete genealogy does not exist and never will exist. There is no continuous record. Zoologists can only infer the degrees of affinity of species by their greater or less structural resemblance to one another, aided by the very imperfect and fragmentary evidence of descent furnished by extinct forms whose remains have been preserved in a fossil state. Any system of classification, therefore, depends, in the first place, on the extent of our knowledge of the structural differences which obtain among species, and in the second place, upon the judgment shown by the framer of the system in grouping together or separating species according to their greater or less resemblances and differences. Consequently there is no such thing as a final scheme of classification of any group. Systems must change with the increase of our knowledge and according to the varying judgments of the authors who frame them. It also follows that there is more certainty about the affinities of species and genera than of the higher divisions, for it is easier to recognise near than remote relationships. In fact, the limits assigned to classes, orders, and families are somewhat arbitrary, and these divisions in different phyla of the animal kingdom do not imply equal degrees of affinity. Thus the classes in one phylum may stand in much closer relationship to one another than classes in another phylum.

If there were a complete genealogical record it would be possible to make the various grades of classification correspond to degrees of relationship; but, as the record cannot be complete, such a correspondence is impossible, and we can only deal according to the best of our judgment with the evidence at our disposal. A classification, then, can only be regarded as an approximate representation of animal affinities; but, such as it is, it should represent the fullest extent of our knowledge. Classifications must change as knowledge advances.

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[The names of species, genera, families, orders, etc., are printed in Italics.]

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